VOLUME 8 NUMBER 6

GENETICS

A PERIODICAL RECORD OF INVESTIGATIONS
BEARING ON HEREDITY AND
VARIATION

NOVEMBER, 1923

Published at Menasha, Wisconsin
by the
BROOKLYN BOTANIC GARDEN
Brooklyn, New York, U. S. A.

GENETICS

A Periodical Record of Investigations Bearing on Heredity and Variation

EDITORIAL BOARD

GEORGE H. SHULL, Managing Editor
Princeton University

WILLIAM E. CASTLE
Harvard University

EDWARD M. EAST
Harvard University

EDWIN G. CONKLIN
Princeton University

ROLLINS A. EMERSON
Cornell University

CHARLES B. DAVENPORT
Carnegie Institution of Washington

HERBERT S. JENNINGS
The Johns Hopkins University

BRADLEY M. DAVIS
University of Michigan

THOMAS H. MORGAN
Columbia University

RAYMOND PEARL
The Johns Hopkins University

GENETICS is a bimonthly journal issued in annual volumes of about 600 pages each. It will be sent to subscribers in the United States, the Philippines, Porto Rico, etc., for $6 per annum for the current volume and for $7 per volume for completed volumes. Canadian subscribers should add 25 cents and other foreign subscribers 50 cents for postage. Single copies will be sent to any address postpaid for $1.25 each.

Back volumes 1 to 6 are for sale by WILLIAMS & WILKINS COMPANY, Baltimore, Maryland.

All subscriptions, notices of change of address, remittances, and business correspondence (except concerning volumes 1 to 6) should be sent to GENETICS, Menasha, Wisconsin, U. S. A., or BROOKLYN BOTANIC GARDEN, Brooklyn, New York. All remittances should be made payable to GENETICS.

Entered as second-class matter August 31, 1922, at the postoffice at Menasha, Wisconsin, under the act of March 3, 1879.

GENETICS

A PERIODICAL RECORD OF INVESTIGATIONS
BEARING ON HEREDITY AND
VARIATION

VOLUME 8 - 1923

PUBLISHED BY THE
BROOKLYN BOTANIC GARDEN
BROOKLYN, NEW YORK
U. S. A.

GENETICS

A PERIODICAL RECORD OF INVESTIGATIONS
BEARING ON HEREDITY AND
VARIATION

EDITORIAL BOARD

GEORGE H. SHULL, MANAGING EDITOR
Princeton University

WILLIAM E. CASTLE
Harvard University

EDWARD M. EAST
Harvard University

EDWIN G. CONKLIN
Princeton University

ROLLINS A. EMERSON
Cornell University

CHARLES B. DAVENPORT
Carnegie Institution of Washington

HERBERT S. JENNINGS
Johns Hopkins University

BRADLEY M. DAVIS
University of Michigan

THOMAS H. MORGAN
Columbia University

RAYMOND PEARL
Johns Hopkins University

PRINTED BY
THE COLLEGIATE PRESS
GEORGE BANTA PUBLISHING CO.
MENASHA, WISCONSIN

TABLE OF CONTENTS

JANUARY NUMBER

(Issued May 14, 1923)

PAGE

Portrait of WILHELM LUDWIG JOHANNSEN ..... Frontispiece

LITTLE, C. C., and JONES, E. E., The effect of selection upon a Mendelian ratio 1

MANN, MARGARET C., The occurrence and hereditary behavior of two new dominant mutations in an inbred strain of *Drosophila melanogaster* 27

HARRIS, J. ARTHUR, and LEWIS, H. R., The correlation between the time of beginning and the time of cessation of laying in the first and second laying year in the domestic fowl 37

BENEDICT, R. C., New bud sports in Nephrolepis 75

MARCH NUMBER

(Issued May 28, 1923)

CLAUSEN, R. E., and GOODSPEED, T. H., Inheritance in *Nicotiana Tabacum*. III. The occurrence of two natural periclinal chimeras 97

WOODWORTH, C. M., Calculation of linkage intensities where duplicate factors are concerned 106

FROST, HOWARD B., Heterosis and dominance of size factors in Raphanus 116

SHULL, GEORGE H., Further evidence of linkage with crossing over in Oenothera 154

KAKIZAKI, YÔICHI, Linked inheritance of certain characters in the Adzuki bean 168

MAY NUMBER

(Issued July 24, 1923)

SAX, KARL, and GÔWEN, JOHN W., Permanence of tree performance in a clonal variety and a critique of the theory of bud mutation 179

COLLINS, J. L., and MANN, MARGARET C., Interspecific hybrids in Crepis. II. A preliminary report on the results of hybridizing *Crepis setosa* Hall. with *C. capillaris* (L.) Wallr. and with *C. biennis* L. 212

TABLE OF CONTENTS

(CONTINUED)

DE VRIES, HUGO, and BOEDIJN, K., On the distribution of mutant characters among the chromosomes of *Oenothera Lamarckiana* 233

WRIGHT, SEWALL, The theory of path coefficients—a reply to Nile's criticism 239

NILES, HENRY E., The method of path coefficients—an answer to Wright 256

BOSHNAKIAN, SARKIS, The relation of the spelt factor in wheat to rachis internode characters 261

WARD, LENORE, The genetics of curly wing in Drosophila. Another case of balanced lethal factors 276

JULY NUMBER

(Issued November 21, 1923)

SAX, KARL, The relation between chromosome number, morphological characters and rust resistance in segregates of partially sterile wheat hybrids 301

UDA, HAJIME, On "maternal inheritance" 322

CHILD, C. M., Physiological polarity and symmetery in relation to heredity 336

MAVOR, JAMES W., An effect of X-rays on the linkage of Mendelian characters in the first chromosome of Drosophila 355

LEFEVRE, GEORGE, and RUCKER, E. H., The inheritance of spangling in poultry 367

HEPPNER, MYER J., The factor for bitterness in the sweet almond .. 390

SEPTEMBER NUMBER

(Issued December 22, 1923)

JENNINGS, H. S., The numerical relations in the crossing over of the genes, with a critical examination of the theory that the genes are arranged in a linear series 393

SAX, KARL, and GOWEN, JOHN W., The place of stocks in the propagation of clonal varieties of apples 458

ANDERSON, E. G., and EMERSON, R. A., Pericarp studies in maize. I. The inheritance of pericarp colors 466

REYNOLDS, BRUCE D., Inheritance of double characteristics in *Arcella polypora* Penard 477

TABLE OF CONTENTS

(CONTINUED)

NOVEMBER NUMBER

(Issued February 7, 1924)

GEROULD, JOHN H., Inheritance of white wing color, a sex-limited (sex-controlled) variation in yellow Pierid butterflies.... 495

SAX, KARL, The association of size differences with seed-coat pattern and pigmentation in *Phaseolus vulgaris*..... 552

DEMEREC, M., Inheritance of white seedlings in maize..... 561

TALIAFERRO, W. H., and HUCK, J. G., The inheritance of sickle-cell anaemia in man..... 594

CORRIGENDA

VOLUME 8, 1923

Page 165, line 11, for "1922" read "1923."
Page 165, line 20, for "1919" read "1909."
Page 167, line 14, for "190" read "1909."
Page 170, table 1, column 7, for "Brown" read "Blackish-brown."
Page 172, table 2(C), column 2, No. 13, for "5" read "4."
Page 173, table 2(E), total, for "174" read "172."
Page 176, line 8, for "B for the color" read "B for the blackish-brown color."
Page 176, line 2 from bottom, for "$\left.\begin{matrix}1\\2\end{matrix}\right\}$3" read "$\left.\begin{matrix}2\\1\end{matrix}\right\}$3."
Page 176, last line, for "*ps ps IB Ib*" read "*ps ps Ib Ib*."
Page 329, line 25, for "the ratio of 3 normal-colored to 1 brown egg" read "only normal-colored eggs."
Page 532, line 12, for "FREYER" read "FRYER."
Page 536, line 4, for "FREYER" read "FRYER."
Page 536, line 39, for "FREYER" read "FRYER."
Page 537, line 2, for "FREYER" read "FRYER."
Page 537, line 5, for "FREYER" read "FRYER."
Page 537, line 23, for "FREYER" read "FRYER."
Page 537, line 24, for "FREYER" read "FRYER."
Page 537, line 25, for "FREYER" read "FRYER."
Page 537, line 30, for "FREYER" read "FRYER."
Page 547, line 11, for "FREYER" read "FRYER."
Page 550, line 23, for "FREYER" read "FRYER."

WILHELM LUDWIG JOHANNSEN

(FRONTISPIECE)

WILHELM LUDWIG JOHANNSEN was born in Copenhagen on February 3, 1857, and died there November 11, 1927. He was the son of an officer of the Danish Army, Colonel OTTO JOHANNSEN, who belonged to a Schleswig family which had given many members to the Danish Civil Service. In 1872 WILHELM left the Realschule in Elsinore, where his father was then stationed, and entered an apothecary's shop as an apprentice, passing the Gehülfenexamen four years later. After practicing his profession in Denmark and Germany for several years he took the State's examination in Pharmacy at Copenhagen in 1879. In 1881 he became an assistant in the chemical division of the CARLSBERG LABORATORY, working under the famous chemist JOHANN KJELDAHL, and became inclined more and more toward a career in pure science. He published his first scientific contribution in 1883 entitled "Om de saakaldte Glutenceller" in the "MEDDELELSER FRA BOTANISK FORENING." The years spent at the CARLSBERG LABOTATORY were rich in scientific work. He began then his important studies on the changes occurring during the ripening and germination of plants and was conducted into studies on the effects of narcotics on the resting period. These studies resulted in 1893 in his discovery of a method of breaking the resting period at an earlier time than normal by means of ether.

In 1888 JOHANNSEN left the CARLSBERG LABORATORY and for nearly five years, while waiting for the establishment of a Lectureship in Plant Physiology at the Landwirtschäftlichen Hochschule in Copenhagen, he resumed his student life in foreign universities, working with PFEFFER at Tubigen and at Darmstadt, Zurich and Vienna. He received the lectureship in 1892 and in 1903 was made a full Professor. In 1905 he was called to succeed his former teacher PEDERSEN as Professor of Plant Physiology and Director of the Institute of Plant Physiology at the UNIVERSITY OF COPENHAGEN.

JOHANNSEN published his last original contribution in Plant Physiology in 1897, a large book, "On the antagonistic effects of the change of matter, especially during ripening and rest." The previous year his first genetic paper had appeared, a short popular summary "On heredity and variability." He started his experimental investigations on barley and beans in 1898 and in 1903 his classical paper "Erblichkeit in Population und in reinen Linien" appeared. From this date on JOHANNSEN concentrated his entire interest on problems of Genetics.

JOHANNSEN was the first to show the difference in the effects of selection upon a general population and within a "pure line." In the former case the selection can alter the proportion of the several types in the population and, if conditions of reproduction are satisfactory, can isolate different "pure lines." Within the "pure line", however, the ancestral regression is complete and selection has no further effect. This paper, appearing the year that MENDEL'S work was rediscovered, greatly stimulated interest in the problems of heredity. In the next few years JOHANNSEN concentrated his attention upon expounding his principles rather than upon experimental investigations and wrote his well-known text book "Elemente der exakten Erblichskeitslehre," the first edition appearing in 1905, the second in 1913 and the third in 1926. This text book well illustrates JOHANNSEN'S personal evolution. In the first edition he lays emphasis mainly upon the "pure lines;" later on the Mendelian crosses; and only still later did he turn to the importance of cytology for the understanding of Genetics.

In 1912 JOHANNSEN lectured in the United States. In his later years he became interested in historical problems. To this period belongs his book "Arvelighed i historisk og eksperimental Belysning," 1918.

INHERITANCE OF WHITE WING COLOR, A SEX-LIMITED (SEX-CONTROLLED) VARIATION IN YELLOW PIERID BUTTERFLIES

JOHN H. GEROULD
Dartmouth College, Hanover, New Hampshire

Received May 24, 1923

TABLE OF CONTENTS

	PAGE
INTRODUCTION	495
Terminology	497
Acknowledgments	498
Previous investigations	499
Inbreeding heterozygotes; narrative of experiments since 1910	500
Homozygotes for white	502
Homozygotes inbred and later developments	503
Types of mating	505
Discussion of the regular ratios in tables 1 to 6	505
Unexpected ratios	508
Résumé	519
A 7 : 9 ratio	519
Stability and proportions of the white variety in the general population	520
Breeding experiments with other species of Colias	526
Colias christina Edw	526
Colias myrmidone Esp	528
White wing color and climate	529
Comparisons with Papilio	532
Sex-controlled characters in *Argynnis paphia* and *Bruchus quadrimaculatus*	537
Some facts and problems of sex physiology. Comparative velocity of development	541
Summary	544
SUMMARY AND CONCLUSIONS	547
LITERATURE CITED	550

INTRODUCTION

The study of polymorphism in butterflies opens up problems of great interest to the student of evolution and heredity. The different varieties of a polymorphic species that are differentiated by genetic rather than by environmental factors may represent, as DARWIN long ago pointed out, possible incipient species. Such variations are now generally believed to have arisen, not by a long process of natural selection of minute changes, but by a comparatively simple and direct process of mutation involving very few genetic changes.

GENETICS 8: 495 N 1923

Second Printing 1965 / University of Texas Printing Division, Austin

These variations in butterflies are in many cases sex-limited, or, to use GOLDSCHMIDT'S term, sex-controlled. They depend upon hereditary factors the effects of which are realized in only one sex, which in the cases thus far studied in Lepidoptera is the female, though dimorphism in the male is known to occur (Lycaenidae, Arctiidae).

Studies upon sex-limited characters show that the differentiating genes, though determining the coloration of the female only, are transmitted, not by sex-linkage in "criss-cross" fashion, but equally by both sexes, like any other non-sex-linked character. The phenotypically uniform male carries and transmits to both sexes of his offspring the determiners of one or another of the different types of female.

Cases of sex-limited dimorphism in the female are not infrequent among Pierid butterflies, and, so far as I have investigated them, they correspond genetically in all essential respects to the polymorphism of the tropical Papilios with three types of female. In addition to the ordinary yellow (or orange) female in several species of Colias, a white variety occurs. This is true not only of *Colias philodice* and *C. eurytheme*, which I have bred extensively, but also of *C. interior* and *C. christina*, in America, *C. edusa*, *C. myrmidone*, *C. hyale* and other palearctic species. It is true also of the closely related *Terias lisa* of our southern states.

In certain species of arctic or sub-arctic distribution, such as *C. interior*, the white variety is said to be more common than the yellow, while in other species (*C. scudderi* and *C. pelidne*) all females are white. In *C. philodice* and *C. eurytheme*, however, the white variety is much the rarer, though in restricted localities in New England and New York the two forms of the female *philodice* are said to be about equally abundant.

Nearly every summer and sometimes a part of the following winter, for thirteen years, I have bred the white female variety of *C. philodice* and that of *C. eurytheme*. *Colias philodice*, the common yellow clover butterfly of the eastern and central northern states, furnished the material for study during the first and last seasons of the study (1908-1911, 1919-1922); *C. eurytheme*, the orange alfalfa butterfly of the western states in 1913, 1914 and 1916; and hybrids between the two species in 1912, 1913 and 1914.

The same genetic phenomena are exhibited in the inheritance of this dominant female variation, white wing color, in both of these species and in hybrids between them. The white variety may be introduced into the species cross from either species, and its inheritance may be studied simultaneously with that of orange *versus* yellow. In 1912 I introduced

white into a species cross through the yellow male of *C. philodice*, in 1914 through the orange male of *C. eurytheme*. Both were sons of white females, but their mates came from strains of the other species that were free from the hereditary factor for the white female coloration.

The term albino sometimes applied to the white female is objectionable because the variation is not due to the lack of pigment, nor is it, like true albinism in mammals and birds, a recessive unrelated to sex. It is rather a dominant sex-limited color variation in the pigment of the scales that furnish the ground color of the wing. This pigment derived from uric-acid products that accumulate in the blood of the pupa (HOPKINS 1906) is normally yellow or orange. The special features of the female wing pattern (broad, yellow-spotted black border, contrasted with the narrow, unspotted border of the male pattern) are unaffected, only the ground color of the dorsal surface of the wings being atypical.

Although white female coloration in *C. philodice* and *C. eurytheme* is a definite and pronounced discontinuous variation, it is suffused in many and indeed in most individuals with a slight, fluctuating tinge of yellow due to secondary factors.

The recessive non-sex-limited variation in larval blood color, blue-green, which appeared recently in my cultures of *C. philodice* (GEROULD 1921), which prevents the appearance of a yellow element characteristic of normal larval skin color, pupal cuticula, the eye of the adult and the egg, is wholly independent of the yellow pigment of the wing scales. The genes determining white wing color and that producing the succession of changes in the life cycle just mentioned, react upon two different yellow pigments both of which are present in the blood of the normal larva and pupa.

Terminology

The term secondary sexual characters has been used in a broad sense to include not only those characters peculiar to individuals of either sex that are secondarily connected with reproduction, like clasping-organs, milk glands, brood-pouches and the like, but also many traits that serve no conceivable function connected with reproduction, like the color patterns and ground color of unisexually dimorphic butterflies.

It has been suggested that the term secondary sexual character should be restricted to those traits and organs obviously connected secondarily with reproduction, like sex differences in genitalia and instincts. If that is done, sex differences not obviously connected in any way with reproduction would naturally be called tertiary sexual characters.

In the present study, however, I have used the term secondary sexual character in the broader sense, as including these tertiary sexual, or sex-limited, characters.

Unfortunately the term sex-limited has had a chequered history, having been applied loosely to several different things. Sex-linked characters, subject to "criss-cross" inheritance, shuffled from one sex to another in two successive generations, were for a time, especially in Europe, called sex-limited, a confusion which MORGAN (1914) long since corrected. A character that shows sex-reversal of dominance, namely, horns in sheep, has been treated by WENTWORTH (1912, 1916) and others, as a *typical* sex-limited character.

GOLDSCHMIDT and FISCHER (1922) have recently proposed the word "sex-controlled" as applying to the varieties of unisexually polymorphic butterflies, the factors for which are transmitted equally by either sex, though realized phenotypically only in one. While this term is not specifically descriptive, for sex-reversed dominance in sheep is of course also sex-controlled, it has the advantage of being free from confusing connotations and capable of serving as a technical term for this type of heredity.

The genes for sex-controlled characters do not express themselves in the male in the cases thus far studied. Their development and hence their realization, is forestalled and inhibited by the development of the characters of that sex. They are latent in the male, patent in the female, sex-controlled in the sense of being concealed or revealed by the more fundamental phenomenon of sex. In the present paper I use the term "sex-limited" as applying to unisexual polymorphism in the same sense that GOLDSCHMIDT now uses the word "sex-controlled."

Acknowledgments

The long course of these experiments has been very much facilitated by financial support generously provided by the CARNEGIE INSTITUTION OF WASHINGTON through the kindness of Dr. C. B. DAVENPORT and the late Dr. ALFRED G. MAYOR. The friendly coöperation of Dr. P. W. WHITING has been of inestimable value to me in the prosecution of the experiments and criticism of some of the results. Among those who have assisted me, Mr. ROLF C. SYVERTSEN and Mr. LLOYD C. FOGG, each of whom has devoted a summer to the work, deserve my appreciative and very hearty thanks.

The live material for the study of *C. eurytheme* was kindly furnished by Messrs. V. L. WILDERMUTH and R. N. WILSON of the Entomological Station of the U. S. DEPARTMENT OF AGRICULTURE at Tempe, Arizona.

PREVIOUS INVESTIGATIONS

In an earlier paper (GEROULD 1911) I showed that the wild white female of *C. philodice*, at least in those localities from which my stock has come, invariably has been a white (yellow) heterozygote, producing, when mated with a male from a stock devoid of white females, equal numbers of white and yellow daughters. Thus white is dominant in the female. About 50 percent of the sons of any white female, though yellow, are heterozygous for white female coloration. Hence yellow was then regarded as dominant in the male, and it was assumed that if white males should appear in appropriate cultures, as they do sometimes in nature, they would be the male recessives for this pair of factors. I now have evidence that this view was incorrect, that the white variation affects only the pigments of the female, and that the male, whether homozygous for feminine whiteness or for yellowness, or heterozygous for both factors determining female coloration, is constantly yellow. Male yellowness and color pattern, accordingly, are inherited quite independently of yellowness in female coloration, just as the male color pattern of the Papilios is inherited independently of the coloration of their polymorphic females.

Thus the yellow sons of a white female represent the three possible classes of female coloration: (1) homozygous white, (2) heterozygous white, (3) recessive yellow. Matings of classes (2) and (3) with pure yellow (recessive) females were recorded in my earlier paper.

The male heterozygous for white (class 2) mated to a pure yellow (recessive) female was found to produce white and yellow daughters in equal numbers; mated to a heterozygous white female the proportion of white daughters to yellow was not then found to be 3 : 1, as would be expected, but 2 : 1, due to the absence in my cultures of homozygous white females, owing, as I believed, to a lethal reaction associated with this combination, comparable to that which eliminates homozygous yellow mice. Only by improving my methods of breeding, and after several years of experimenting, have I finally succeeded (in 1920) in securing from a mating of this sort a brood showing a definite, clear-cut ratio of three white females to one yellow, from which I have been able to select and breed for two successive generations a stock in which all the females are white.

The male (class 3) homozygous for yellow female coloration, as I showed in my earlier paper, if mated to a yellow recessive female, produces only yellow recessive daughters; if mated to a heterozygous white female, equal numbers of white and yellow daughters.

The male homozygous for white female coloration (class 1) had not been bred in 1911, but in 1920, as just stated, I succeeded in breeding for the first time a family that contained in all probability 25 percent of homozygous white females and, accordingly, an equal percentage of males homozygous for white, though phenotypically yellow because they showed the epistatic male coloration. These males, homozygous for white, mated with their white sisters, homozygous or heterozygous for the dominant white female color, produced two successive generations of white females only.

The only remaining combination, namely homozygous recessive yellow female × male homozygous for white, which, of course, should also produce white daughters only, was made in 1920, but the resulting brood of caterpillars perished in hibernation. And on testing the only brood of all white females that came through the winter of 1920-1921, namely, brood ϵ, by mating them in May 1921 with wild white-free males, I discovered that every one of the four white females that were tested was heterozygous for white (giving broods e, p, i, s) throwing equal numbers of white and of yellow offspring.

INBREEDING HETEROZYGOTES; NARRATIVE OF EXPERIMENTS SINCE 1910

Although it is a comparatively simple matter to breed large families from parents of the spring generation emerging late in June or early in July and to start from this early summer generation a set of families to eclose in August-September, it is most difficult to bring these latter families of caterpillars through to maturity. The polyhedral, or wilt, disease is the chief obstacle, which, even with constant vigilance and various measures for sterilization, I have been able only partially to overcome.

Beginning the narrative of experiments with the unpublished results of 1911, one brood produced by inbreeding that year is of some interest. The first of two generations descended from a white female of *C. philodice* gave equal numbers of heterozygous white and recessive yellow daughters (1911, $\gamma = 28$ white ♀♀, 21 yellow ♀♀, 42 ♂♂. (See conspectus of matings.) The sons consequently may be assumed to have been likewise heterozygous (white-yellow) and recessive (yellow-yellow) for female coloration. One of them, γ^4♂, was tested by mating him to a homozygous yellow female and found to be heterozygous for female coloration (giving 1911, χ, 1 white ♀, 2 yellow ♀♀, 13 ♂♂. He was again mated to a heterozygous white sister (γ^{29}♀) and produced four white daughters, none yellow. Obviously the numbers were too small to bring out the expected 25 percent of recessive yellow daughters.

The experiments of the following years with white *eurytheme* stock inbred, gave likewise three small families the father of each of which, like the mother, was heterozygous for white, and which gave only white daughters, not a 3 : 1 nor a 2 : 1 ratio, (1913, e, f, h). One of these, 1913, e, contained as many as nine white females. It is remarkable that no yellow female appeared in this brood. The other two families (f and h) each contained only three white females. More reliable than these small broods, however, was 1913, t, a species back-cross between a white *C. eurytheme* ♀ × a species hybrid (*eurytheme* × *philodice*) ♂. This brood comprised 39 white females, none yellow (and 33 males)! The hybrid male parent, o^{124} ♂, and the female, a^{5} ♀ (white), were both members of broods made up of 50 percent heterozygous white and 50 percent homozygous recessive yellow individuals, his sisters (of brood o) being actually 36 white, 35 yellow; hers (of brood d) 4 white and 4 yellow. I shall try to explain these anomalous cases, which are remarkable for the absence of recessive yellow individuals, in a later section (page 518).

These puzzling cases led to repeated attempts to inbreed white-bearing stock both of *C. eurytheme* and of *C. philodice*. Although the experiments of 1914 were mostly directed toward the study of orange *versus* yellow in hybrids of the two species, two matings deserve special notice. A son of a heterozygous white female *eurytheme* from Arizona (namely, y^{41} ♂, of a brood made up of 13 white and 15 yellow sisters) was mated with a *philodice* female (z^{26} ♀) of a strain homozygous for yellow, and produced 7 white, 9 yellow daughters (1914,c). He was evidently heterozygous for white female coloration and transmitted it to half of his species-hybrid daughters. This case was perfectly clear, but a reciprocal cross of the same two strains gave (in family a) a peculiar result. A male *philodice* of the same homozygous yellow strain (z^{13} ♂) was mated with white female *eurytheme* (y^{44} ♀), of the brood composed of 13 white and 15 yellow females, which should have produced, therefore, equal numbers of white and yellow daughters. The result, however, was 24 white females : 10 yellow females and 20 males (brood 1914, d). This case also will be discussed under "Unexpected ratios" (see page 514).

The two families of inbred white obtained in 1916 (II and III) from *eurytheme* stock, gave a precisely 50 : 50 ratio of white and yellow females, showing that the males used in mating were homozygous recessives for female coloration, so that no light was thrown on the problem of mating together two heterozygotes and no progress made toward securing homozygous white stock.

The difficulty in getting conclusive evidence regarding the second generation, due to the wilt or polyhedral disease, which strikes the inbred stock in midsummer very severely, was obviated in 1919 and 1920 by using caterpillars of *C. philodice* (from white mothers of the previous fall generation) that I had succeeded in hibernating, so that, by breeding from their imagines the last of May, a large generation of adults was obtained in June-July. The evidence in 1919 pointed to the fact that the only male (son of a white female) that had hibernated (1919, $A^1\sigma$) was homozygous for yellow. He was tested by five matings. With two yellow sisters he produced only yellow daughters (7 by one, 5 by another). By one white sister he had 8 white daughters : 8 yellow daughters (1919, D); by another, 28 white daughters, 38 yellow daughters, and 64 sons (1919,B). So far he was shown to be a perfectly regular homozygous recessive (yellow) for female coloration. The fifth and last mating, with a heterozygous white female, though the male was clearly homozygous for the recessive yellow, gave an unmistakable ratio of 2 white daughters : 1 yellow daughter (1919, C = 67 white females, 36 yellow females and 77 males). This remarkable case also will be fully discussed later (page 515).

HOMOZYGOTES FOR WHITE

The results obtained with *C. philodice* in 1920 were satisfactorily regular. Three of the five sons of a white female, hibernating as caterpillars, were tested by mating them to yellow females, and two of them ($\phi^1\sigma$ and $\phi^2\sigma$) were found to be heterozygous for white, the third (ϕ^3) homozygous for yellow. $\phi^2\sigma$ mated to a yellow sister, $\phi^6\varphi$, gave a brood, λ, consisting of exactly 28 white daughters and 28 yellow daughters (and $77\sigma\sigma$), proving that he was heterozygous for white. Fortunately he had been mated to the only white female that I had succeeded in hibernating as a caterpillar (namely, $\phi^5\varphi$). This female produced an extraordinarily large brood (1920, ι) of 253 butterflies, the females of which showed an unmistakable ratio of 3 white : 1 yellow. The final count was 95 white ♀♀ : 28 yellow ♀♀ : $130\sigma\sigma$; the expectation on a 3 : 1 basis being 92.25 white : 30.75 yellow. Repeatedly during the emergence of this brood the count showed an almost precise 3 : 1 ratio. When 111 females had emerged from the chrysalis, for example, there were 84 white : 27 yellow, 83.25 : 27.75 being the expectation.

Details in regard to this remarkable family, 1920 i, are important not merely because it demonstrated for the first time that the 3 : 1 instead of the 2 : 1 ratio can be obtained from the union of two heterozygotes for white, but because it proves also that *homozygous* white females and *yellow*

males homozygous for white actually result from this combination, as was shown by subsequent breeding.

Moreover, five out of the seven individuals of this brood that were used in breeding proved to be heterozygous for a new blue-green variation in hemolyph and integument color in the caterpillar, in which the suppression of a yellow element in the hemolymph, probably derived from xanthophyl of the food, changes not only the color of the caterpillar and pupa but also the cuticula of the pupa and the eye color of the adult (see GEROULD 1921).

HOMOZYGOTES INBRED, AND LATER DEVELOPMENTS

Our present interest in this brood (1920, ι) in which the 3:1 ratio occurred, lies in the fact that all the three white females that were used in breeding (each mated to a different brother) produced white daughters only (brood $\beta = 24$ white ♀♀, 17♂♂; $\alpha = 2$ white ♀♀, 2♂♂; $\upsilon = 10$ white ♀♀, 7♂♂). The following generation also consisted of white females only (namely, κ(ex β) = 1 white ♀, 1♂; ϵ (ex β) = 15 white ♀♀, 2♂♂; ρ (ex β) = 10 white ♀♀, 14♂♂; δ(ex β) = 2 white ♀♀, 4♂♂; π (ex υ) = 21 white ♀♀, 29♂♂; ω (ex υ) = 4 white ♀♀, 5♂♂; σ(ex υ) = 2 white ♀♀, 8♂♂).

Five of these families containing white females only (ρ, δ, π, ω, σ) were allowed to come through to the butterfly stage in November and December, and no attempt was made to mate and breed them further. The two others (κ and ϵ) survived the winter as caterpillars and were brought to maturity during the last two weeks of April, 1921. Family ϵ consisted of 15 white females and two males, κ of only one (white) female and one male. Since none of these three surviving males could be induced to mate with any of the fifteen white females of brood ϵ, it became necessary, in order to keep the stock alive, to mate the latter with wild males. But, since butterflies of this species had not yet appeared in the field at this high latitude so early in the season, four wild males, by the kind coöperation of Prof. P. W. WHITING, were imported from Annandale-on-Hudson, N.Y., a region further south, where they were then abundant. Received on May 6, these four males were immediately mated with four white females of brood ϵ, producing (June 20 to July 26) the four families, 1921, e, p, i, s.

Since brood ϵ and all the others of its generation were exclusively white, and since the parents of this brood also belonged to an all-white brood, it was expected that the four families produced by crossing this stock with recessive wild males would contain white heterozygous females only. If by a rare chance one of the wild males should carry the factor for white female coloration, the probability of getting all white females would be even more certain.

An unexpected result happened. The four families produced by crossing the all-white stock with wild males, presumably homozygous recessives for yellow female coloration, consisted of approximately 50 percent white (heterozygous) females and 50 percent yellow recessives. In other words none of the four white mothers of the four families, e, p, i, s, was homozygous for white. Every one was heterozygous. The obvious conclusion was that the true-breeding white stock had consisted of equal numbers of homozygous white females and heterozygous white females. Equal chances to mate had been given to nine other sisters placed in the same cage with these four and with the males from New York. Possibly homozygous white females are less inclined to mate than the heterozygous, just as I have found butterflies from blue-green caterpillars to be defective in mating instincts. Since I had secured all the pairs that could be conveniently used for breeding, the other females were not tested, except that two of them (ϵ^5 and ϵ^6) were kept for several days with $\kappa^2\sigma^3$, a butterfly from a blue-green caterpillar, which was not observed to mate though he was kept alive for 26 days. These two females each laid sterile eggs.

My purpose in inbreeding to get the following generation, was double: to seek again the elusive ratio that two heterozygotes for white female coloration should give, and more especially, to recover recessive blue-green caterpillars, for whose factor I had reason to believe half of the individuals of the two previous generations of 1921 were heterozygous. For this inbreeding, members of the largest family, 1921, p, consisting of 65 white females 69 yellow females and 217 males were chosen. Owing to limitations of greenhouse space, I bred from this family only. In six of the nine families thus produced, the progeny showed that the male parent was recessive for female coloration, giving, with the white heterozygous females with which they respectively were mated, equal numbers of white and yellow female offspring; while the three other families (r, o, d) contained in each case such an excess of white daughters as may be interpreted by assuming that the male was heterozygous. One (t), though small (10 white, 2 yellow), probably presents the 3 : 1 ratio uncomplicated by any disturbing factors; another (o) gave a clear-cut 2 : 1 ratio (49 white, 25 yellow);[1] the third (d) gave only white female offspring. The two last, as I shall show in a later section (page 517), may be explained on the hypothesis of a lethal factor linked with yellow.

[1] This aberrant ratio may even better be regarded as a modified 1:1, assuming that the father was *homozygous* for yellow and that both parents were heterozygous for a lethal factor closely linked with yellow (see page 517 for a full discussion).

This generation of butterflies, 1920, p, emerged in August, and consisted of individuals with olive-green and blue-green eyes (from olive-green and blue-green caterpillars), as well as those apparently normal (as regards those mutations). Consequently, attention was directed for the rest of the season to breeding these two sets of mutants in caterpillar color, without special regard to white wing color.

Nevertheless, 17 matings of white females were made in spite of somewhat diminished mating affinity. Thirteen white females that had been mated, either with males of this stock or with wild males, were tested as to their ability to lay fertile eggs. The majority of them (8) laid only sterile eggs; four laid well, but only two of these had been mated to males of this inbred stock. It is evident from these facts that inbreeding was producing in this generation a high percentage of infertility. Females from olive-green caterpillars were probably no more deficient in mating affinity or fertility than those from grass-green caterpillars, but females from blue-green caterpillars lacked in both mating affinity and fertility.

The hemolymph variations of the caterpillar, however, though affecting the eye color of the butterfly, are entirely independent of white wing color, to which we now recur. Only one family (1921, a) of the succeeding (September-October) generation is of much significance as regards the inheritance of white wing color. It came from the large family of the August generation showing the clear-cut 2 : 1 ratio (i.e., 1921, o = 49 white females, 25 yellow females, 80 males), and it contained white females only. The explanation of this is the occurrence in the parents of a lethal factor linked to that for the recessive yellow, as will be brought out later (see page 517).

This brings the stock to the close of the season of 1921, when it was put into winter quarters. Adverse weather conditions (excessively dry soil, and possibly the unusually prolonged periods of intense cold) destroyed all the hibernating caterpillars of this most interesting stock, that had been put underground, save a few that had been packed away with vegetables, which furnished the necessary protection against drought and cold. But these few were already infected with wilt and died in the spring before reaching maturity.

TYPES OF MATING

Discussion of the regular ratios in tables 1 to 6

In inheritance of female whiteness, that depends primarily on a single factor difference, there are only three types of individuals as far as genetic constitution is involved, namely, the homozygous and the heterozygous

dominants and the recessive. In one sex these genetic differences are expressed as two phenotypes (dominant and recessive), whereas in the other they are entirely latent, masked by the stronger yellow color peculiar to that sex.

Dominant white female coloration, the gene for which we will call *W*, is contrasted with the recessive normal yellow ground color, the gene for which we will call *w*. Females are therefore either white (*WW*, *Ww*) or yellow (*ww*). Males, constitutionally of all three types of female coloration (*WW*, *Ww* and *ww*) occur in the butterfly population with frequencies corresponding to those of the female types existing in that particular region.

Owing to the comparative rarity of the white female in the locality where I have worked, individuals of either sex that are homozygous for the dominant-white female color are exceedingly rare, heterozygotes more common.

The following combinations are represented in my cultures:

White female, *Ww*, male *ww*, shown in table 1
White female, *Ww*, male *Ww*, shown in table 2
White female, *Ww*, male *WW*, shown in table 3
White female, *WW*, male *Ww*, shown in table 3
Yellow female, *ww*, male *ww*, shown in table 4
Yellow female, *ww*, male *Ww*, shown in table 5

It is evident that three possible combinations of homozygous white stock are missing, or not distinguishable from the $Ww \times WW$ combination which of course breeds true to female whiteness. This is due partly to the fact that it is exceedingly difficult to carry on the same stock for several generations and partly to the fact that, when in 1920 an abundance of true-breeding white stock was secured in a third generation of inbreeding, an interesting variation in caterpillar color appeared that temporarily diverted my attention from the original problem. Winter came on, and the particular caterpillars of true-breeding all-white stock that survived proved to be not homozygotes but heterozygotes for white. Thus, it is uncertain whether females of the *WW* type have been mated with *WW*, and it is evident that *WW* females have not yet been crossed with *ww* males, nor yellow *ww* females with *WW* males. As I am convinced that there is nothing inherently lethal in the *WW* combination, this should be a matter of no difficulty when homozygous white stock is again obtained by the repeated inbreeding of heterozygotes.

Wild white females of *C. philodice*, as well as of *C. eurytheme*, have invariably proved to be heterozygous for white female coloration. Twelve

of *philodice* and four of *eurytheme* are included in table 1. The chances of a wild white female's mating with anything but a homozygous yellow male are very small, about 1 : 20 in such a population as that with which I have worked, in which yellow females outnumber the white by about twenty to one,[2] and in which the male population, though always yellow, presumably corresponds to the female in respect to the transmission of yellow or of white female coloration.

The proportion 50 : 50 runs uniformly, with few exceptions, through the long list of families noted in table 1, giving a total of 635 white : 639 yellow for the two species and their hybrids.

Thirty-two families of *C. philodice* are listed in table 1 and three showing well-marked exceptions to this ratio (see page 510) will be discussed in the next section. The 10 broods of *C. eurytheme* show a slight excess in favor of white females, and the species hybrids, if we subtract the one anomalous brood, 1914 d, (to be discussed in the following section), show exactly 100 white and 100 yellow females.

The combination $Ww \times Ww$ shown in table 2 has presented such irregularities that, until I bred 1920, ι, I doubted the possibility of getting with this combination in *C. philodice*, a clean-cut 3 : 1 ratio. But in this brood there was no evidence of disturbing factors. The fact that three broods showing irregularities (1921, o, a, d) were descended from this perfectly regular brood is to be accounted for by the assumption that the wild ♂ (w^3) with which the stock (ϵ^2 ♀) was out-crossed in the spring of 1921 was probably heterozygous for a lethal factor. The total, 105:30, for the two $Ww \times Ww$ broods is close to expectation. The exceptional broods under II and III will be fully discussed in the next section.

Table 3 shows the exclusively white descendants of the brood, 1920, ι, that distinctly showed the 3:1 ratio. Accordingly, one or both parents of succeeding broods (producing in turn κ, ϵ, ρ, δ) and υ (producing π, ω, σ) were homozygous. The oncoming of winter permitted the testing of only one of these all-white families, namely, ϵ, of which all four females that were tested (by mating with wild males homozygous for yellow female coloration) proved to be heterozygous for white, since their offspring (1921, e, p, i, s; see conspectus of matings) contained equal numbers of white and yellow females. For if these four females of family ϵ had been homozygous for white, they would have produced, of course, white daughters only, whether their wild mates were, or were not, carriers of the gene for white female coloration.

[2] Possibly ten to one would be a more correct estimate (see page 520).

Table 4 shows that yellow females, *ww*, mated with males homozygous for the recessive yellow factor have only yellow daughters. The nine broods of *C. philodice* here listed are a by-product of the cultures, and represent only a small part of all the numerous families that I have raised from wild females. This is the usual experience in this region, where white females are comparatively rare. The same is true for large broods of orange-colored *C. eurytheme* raised from females from Arizona and Colorado, three of which are listed, and for hybrids between *C. philodice* and *C. eurytheme*, of which six broods are recorded.

Table 5 shows that the recessive yellow female mated with a male heterozygous for female whiteness produces equal numbers of white and yellow daughters. This is true both of *C. philodice* and hybrids between *philodice* and *eurytheme*. Two anomalous broods are recorded, namely, 1920, o, in which there was such a shortage of white females that the ratio stands as 7 : 9 (59 white : 76 yellow) and 1910, i (30 white : 14 yellow), which will be discussed in the following section.

The shortness of the list of families of yellow females throwing equal numbers of white and yellow daughters is due merely to the fact that white females were usually bred, rather than yellow, the latter being used only to test the genetic constitution of certain males or because the yellow mother had some remarkable coloration, as for example the wild female of 1909 that resembled *Colias nastes* of Labrador and the Far North, which gave family 1909, b, containing only normal yellow and normal white daughters. It would have been an easy matter, if adequate greenhouse space had been available, greatly to extend the list shown in table 5.

Unexpected ratios

Even in the earlier years of the investigation I was struck with the not infrequent appearance of the 2 : 1 ratio in broods in which either 1 : 1 or 3 : 1 was expected, but the numbers involved were then so small that it was doubtful whether they accurately represented the genetic constitution of the parents.

The difficulty in obtaining a 3 : 1 ratio from two heterozygous parents has been sufficiently emphasized in previous sections. In 1911, when my preliminary paper appeared, the available evidence led to the conclusion that the homozygous white (*WW*) combination is lethal. This evidence consisted merely in the two families, 1910 g and h, which together gave 51 white : 30 yellow female offspring. The male parent of these broods, as well as the two mothers, was very definitely a heterozygote for female coloration, and the theoretical expectation 54 : 27 on a 2 : 1 basis was much more closely approached than 60.75 : 20.25 on a 3 : 1 basis.

TABLE 1

♀ *Ww* × ♂ *ww*. *Heterozygous white* ♀ × ♂ *homozygous recessive for white female coloration.*

	MOTHER	FATHER	BROOD	WHITE ♀ ♀ *Ww*	YELLOW ♀ ♀ *ww*	MALES
C. philodice						
1908	Wild	Wild		2	3	3
1909	Wild	Wild	1a	7	16	39
	Wild	Wild	2w	8	4	20
	Wild	Wild	c	3	7	13
1910	Wild	Wild	a	6	9	18
	Wild	Wild	b	22	28	79
	4b[21]	4b[15]	m	5	3	9
	lb[39]	lb[31]	o	3	4	9
	Wild	Wild	c	8	8	24
	Wild	Wild	d	15	13	30
1911	Wild	Wild	α	8	17	28
	Wild	Wild	β	13	11	25
	Wild	Wild	γ	28	21	42
	γ[41]	γ[3]	ε	3	2	10
	γ[31]	γ[3]	η	3	5	1
	q[2]	q[1]	R	4	5	8
1919	Wild	Wild	A	3	4	1
	A[2]	A[1]	B	28	38	64
	A[3]	A[1]	D	8	8	26
1920	Wild	Wild	φ	1	3	5
	O[13]	O[1]	μ	14	10	20
1921	e[1]	Wild[1]	e	6	11	22
	e[2]	Wild[2]	p	65	69	217
	e[8]	Wild[2]	i	1	1	1
	e[7]	Wild[4]	s	3	4	9
	p[42]	p[14]	r	5	6	16
	p[45]	p[56]	f	20	13	40
	p[209]	p	y	3	3	8
	p[212]	p[177]	c	14	9	45
	p[215]	p[170]	h	13	12	26
	p[216]	p[173]	q	21	17	36
	+0[1]	+0[7]	l	0	2	1
Total for *C. philodice*				343	366	894
Expected				*354.5*	*354.5*	
C. eurytheme	Wild	Wild	a	29	24	57+1 gyn.
1913	a[18]	a[30]	d	4	4	4
	a[89]	a[83]	j	3	5	3
	Wild	Wild	b	27	20	49
	b[53]	b[48]	m	16	11	38
	b[59]	b[33]	n	1	2	1
1914	Wild	Wild	y	13	15	29
1916	Wild	Wild	I	62	53	102
	I[23]	I[6]	II	28	29	39
	I[18]	I[17]	III	9	10	11
Total for *C. eurytheme*				192	173	333
Expected				*182.5*	*182.5*	

TABLE 1 (continued)

	MOTHER	FATHER	BROOD	WHITE ♀♀ *Ww*	YELLOW ♀♀ *ww*	MALES
Species hybrids 1913	b^{78} (*eurytheme*)	Wild *philodice*	o	36	35	72
	a^{94} (*eurytheme*)	Wild *philodice*	p	4	3	11
	p^{11} (F_1 hybrid)	o^{10} (F_1 hybrid)	q	3	3	13
	m^{28} (*eurytheme*)	o^{112} (F_1 hybrid)	r	4	3	5
	m^{26} (*eurytheme*)	p^{15} (F_1 hybrid)	s	35	38	108
	e^{10} (*eurytheme*)	o^{122} (F_1 hybrid)	u	15	13	36
	m^{12} (*eurytheme*)	Wild *philodice*	v	3	5	25
Total for species hybrids				100	100	270
Grand total				635	639	1497

Anomalous broods showing a lethal factor linked with yellow
♀ *WL.wl* × ♂ *wL.wl* = 2 white : 1 yellow

1914	y^{44} (*eurytheme*)	z^{13} (*philodice*)	d	24	10	20
1919	A^4 (*philodice*)	A^1 (*philodice*)	C	67	36	77
1921	p^{43} (*philodice*)	p^2 (*philodice*)	o	49	25	80
Total				140	71	177
Expected				*140.6*	*70.3*	

TABLE 2

♀ *Ww*×♂ *Ww. Heterozygous white female* × *male heterozygous for white female coloration.*
I. Non-lethal combination (3 : 1 ratio). ♀ *WL.wL*×♂ *WL.wL*

	MOTHER	FATHER	BROOD	WHITE ♀♀	YELLOW ♀♀	MALES
1920	ϕ^5	ϕ^2	ι	95	28	130
1921	p^{41}	p^{21}	t	10	2	19
Total				105	30	149
Expected				*101.25*	*33.75*	

II. ♀ *WL.wl* × ♂ *WL.wl.* All-white families from heterozygous white parents

C. philodice 1911	γ^{29}	γ^4	Δ	4	0	7
1921	$+o^4$	$+o^8$	a	17	0	9
	p^{251}	p^{296}	d	28	0	30
C. eurytheme 1913	a^{59}	a^{27}	e	9	0	15
Hybrids 1913	d^5	o^{124} (hybrid)	t	39	0	33
Total				97	0	94

TABLE 2 (continued)

III. ♀ *Wl.wL*×♂ *WL.wl*. Crossover of lethal factor to white in the female parent. (2 : 1 ratio)

	MOTHER	FATHER	BROOD	WHITE ♀♀	YELLOW ♀♀	MALES
C. philodice						
1910	$1d^{39}$	$1d^{15}$	g	38	22	63
	$1d^{45}$	$1d^{12}$	h	13	8	16
	$1d^{36}$	$1d^{8}$	l	*3*	3	4
Total				54	33	83
Expected				*58*	*29*	

TABLE 3

♀ *Ww*×♂ *WW*, *or* ♀ *WW*×♂ *Ww*, *or* ♀ *WW*×♂ *WW*. *All-white families, partly homozygous.*

	MOTHER	FATHER	BROOD	WHITE ♀♀	YELLOW ♀♀	MALES
C. philodice	ι^{20}	ι^{13}	β	24	0	17
1920	$+\beta^{19}$	$+\beta^{5}$	κ	1	0	1
	$+\beta^{20}$	$+\beta^{5}$	ϵ	15	0	2
	$+\beta^{10}$	$+\beta^{2}$	ρ	10	0	14
	$+\beta^{21}$	$+\beta^{2}$	δ	2	0	4
	ι^{46}	ι^{2}	μ	2	0	2
	ι^{38}	ι^{14}	υ	10	0	7
	υ^{2}	υ^{12}	π	21	0	29
	υ^{3}	υ^{13}	ω	4	0	5
	υ^{14}	υ^{9}	σ	2	0	8
Total				91	0	89

TABLE 4

♀ *ww*×♂ *ww*. *Homozygous recessive yellow* ♀×♂ *homozygous recessive for white female coloration.*

	MOTHER	FATHER	BROOD	YELLOW ♀♀	MALES
C. philodice					
1909	a^{24}	Brother of a^{24}	2y	15	20
1914	Wild	Wild	z	41	47
1919	A^{7}	A^{1}	E	7	13
	A^{5}	A^{1}	F	5	3
1920	ϕ^{8}	ϕ^{3}	ς	118	127
	ι^{101}	ς^{157}	θ	13	21
1921	$-y^{1}$	h^{1}	κ	8	7
	$-o^{29}$	Wild[2]	u	6	10
	o^{77}	Wild[3]	mc*	20	2
Total				233 ♀♀	250 ♂♂

TABLE 4 (continued)

	MOTHER	FATHER	BROOD	YELLOW ♀♀	MALES
C. eurytheme				(orange-yellow)	
1912	Wild, from Arizona	Wild	u	9	4
1913	Arizona	Wild	c	206	214
1914	Arizona	Wild	x	136	149
Total				351 ♀♀	367 ♂♂
Species hybrids					
1912	u^9 (*eurytheme*)	Wild *philodice*	a	11	1
1914	z^{45} (*philodice*)	x^{63} (*eurytheme*)	a	40	122
	a^{101}	a^{102}	e	6	6
	a^{103}	a^{104}	g	12	22
	a^{129}	Wild *philodice*	h	36	24
	h^7	h^3	i	8	14
Total				113 ♀♀	189 ♂♂

*The brood mc is melanic, o^{77} ♀ being a melanic mutant. †The dearth of males was due to the use of the older caterpillars (normal, grass-green) for exhibition purposes and their death.

TABLE 5

♀ *ww* × ♂ *Ww. Homozygous recessive (yellow)* ♀ × ♂ *heterozygous for white female coloration.*

	MOTHER	FATHER	BROOD	WHITE ♀♀	YELLOW ♀♀	MALES
C. philodice						
1909	wild, *nastes*-like	wild	b	5	10	19
1910	a^{14}	a^7	e	13	14	59
	a^{10}	a^{19}	f	7	5	10
	$1d^{30}$	$1d^8$	k	19	19	46
1911	♀ of pure yellow stock	γ^4	χ	1	2	13
1920	ϕ^6	ϕ^2	λ	28	28	77
	ϕ^7	ϕ^1	o	59*	76*	146
Total for *C. philodice*				133	154	370
Expected				*143.5*	*143.5*	
Species hybrids						
1912	u^7 (*eurytheme*)	Wild *philodice*	b	3	1	1
1914	z^{36} (*philodice*)	y^4 (*eurytheme*)	c	7	9	45

*Note the 7 : 9 ratio in 1920, o; one-sixteenth of the ♀♀ (namely white) are missing.

TABLE 5A

wL.wl ♀ × ♂ *WL.wl*. *Both parents heterozygous for a lethal factor linked with yellow.*

	MOTHER	FATHER	BROOD	WHITE ♀♀	YELLOW ♀♀	MALES
C. philodice 1910	1 d^{45}	1 d^{18}	i	30	14	27

TABLE 6

Irregular ratios due to a lethal factor, reassembled.

A. ♀ *WL.wl* × ♂ *wL.wl* = *WL.wL* + *WL.wl* + *wL.wl* + [*wl.wl*, dies]. 2 white : 1 yellow.

	MOTHER	FATHER	BROOD	WHITE ♀♀	YELLOW ♀♀	MALES
Hybrids of 1914	y^{44} (*eurytheme*)	z^{13} (*philodice*)	d	24	10	20
C. philodice 1919	A^4	A^1	C	67	36	77
1921	p^{43}	p^{2*}	o	49	25	80
Totals				140	71	177

*If the ♂ p^2 was *Ww*, this belongs under section *C*. He was not tested.

B. ♀ *WL.wl* × ♂ *WL.wl* = *WL.Wl* + 2*WL.wl* + [*wl.wl*, dies]. All white.

C. philodice 1911	γ^{29}	γ^4	Δ	4	0	7
1921	$+o^4$	$+o^8$	a	19	0	10
	p^{351}	p^{296}	d	28	0	30
C. eurytheme 1913	a^{39}	a^{27}	e	9	0	15
Hybrids 1913	d^5	o^{194} (hybrid)	t	39	0	33
Totals				99	0	95

C. ♀ *Wl.wL* × ♂ *WL.wl* = *WL.Wl* + *WL.wL* + [*Wl.wl*, dies] + *wL.wl*. 2 white : 1 yellow.

C. philodice 1910	1 d^{39}	1 d^{18}	g	38	22	63
	1 d^{45}	1 d^{18}	h	13	8	23
	1 d^{36}	1 d^{8}	l	3	3	4
Total				54	33	90
Expected				*58*	*29*	

D. ♀ *wL.wl* × ♂ *WL.wl* = *WL.wL* + *WL.wl* + *wL.wl* + [*wl.wl*, dies]. 2 white: 1 yellow

1910	1 d^{46}	1 d^{18}	i	30	14	27

Consideration of these two families and the general difficulty of getting the 3:1 ratio from two heterozygotes certainly indicates that lethal factors exist which may be associated with the dominant white factor, but does not prove that the combination *WW* is always lethal. In fact the 2nd, 3rd and 4th generations of 1920 tend to prove the opposite, for in that series of inbred fraternities the ratio 3 white : 1 yellow was obtained unmistakably, followed for two generations by all-white families. Moreover, the mathematical conclusions of Dr. J. W. YOUNG (see page 521) show that, if homozygous white combinations were always lethal, this factor would in the long run, with random mating, disappear from the general population, and I have no evidence that such a process is, or has been, going on.

On the other hand, the experiments of recent years have brought to light families of large size in which the proportions of white to yellow female offspring can best be explained by assuming that a lethal factor is closely associated with the recessive allelomorph of white, namely, yellow, or *w*.

The first of these remarkable families that we shall consider is one in which a heterozygous white female, mated with a certainly homozygous recessive male, produced twice as many white as yellow daughters. In other words, half of the expected yellow daughters were missing, eliminated presumably by a lethal factor closely linked with yellow.

The father (A^1 ♂) in this family, 1919, C, was clearly a homozygous recessive (yellow, *ww*) for female coloration, as two of his matings with yellow sisters and two matings with white sisters (broods B and D) showed.[3] Mated to recessive yellow sisters he gave only yellow daughters, to white sisters both white and yellow daughters in equal numbers.

The fifth mating of this same homozygous recessive male, with another white female (A^4 ♀), produced very definitely two white daughters to one yellow, namely, 67 white, and 36 yellow females [expectation on 2 : 1 basis $68\frac{2}{3}$: $34\frac{1}{3}$], and 77 males. During the eclosion of the brood this tendency to follow the 2 : 1 ratio constantly demonstrated itself as the daily tally was kept. Thus when the total number of females stood at 93, 62 of them were white, 31 yellow.

A similar case occurred five years earlier (1914) when a heterozygous white female of *C. eurytheme* (y [44]) was mated with a male of a brood of *C. philodice* (z) containing only yellow females, a male therefore homozygous for recessive yellow female coloration. The result (1914, d) was not the expected equal numbers of white and yellow, but 24 white and 10

[3] See "Conspectus of matings," 1919; also table 1 (end) and table 6, A.

CONSPECTUS OF MATINGS

C. philodice

1908

Wild
♀Ww X ♂ ww
2 + 3 + 3
Ww ww ♂♂

1909

Wild
♀Ww X ♂ ww
1a = 7 + 16 + 39
Ww ww ♂♂

- ww ww
  a²⁴ ♀ X a ♂
  2y = 0 + 15 + 20
  ww ♂♂
- Ww ww
  1a³⁵ ♀ X 1a⁶ ♂
  2W = 8 + 4 + 20
  Ww ww ♂♂

Wild (*wastes*-like ♀)
♀ww X ♂ Ww
1b = 5 + 10 + 19
Ww ww ♂♂

Wild
♀Ww X ♂ ww
1c = 3 + 7 + 13
Ww ww ♂♂

1910

Wild
♀Ww X ♂ ww
a = 6 + 9 + 18
Ww ww ♂♂

- ww Ww
  a¹⁴ ♀ X a⁷ ♂
  e = 13 + 14 + 59
  Ww ww ♂♂
  - ww Ww
    1e²⁴ ♀ X 1e²³ ♂
    ♀ →
- ww Ww
  a¹⁰ ♀ X a¹⁹ ♂
  f = 7 + 5 + 10
  Ww ww ♂♂

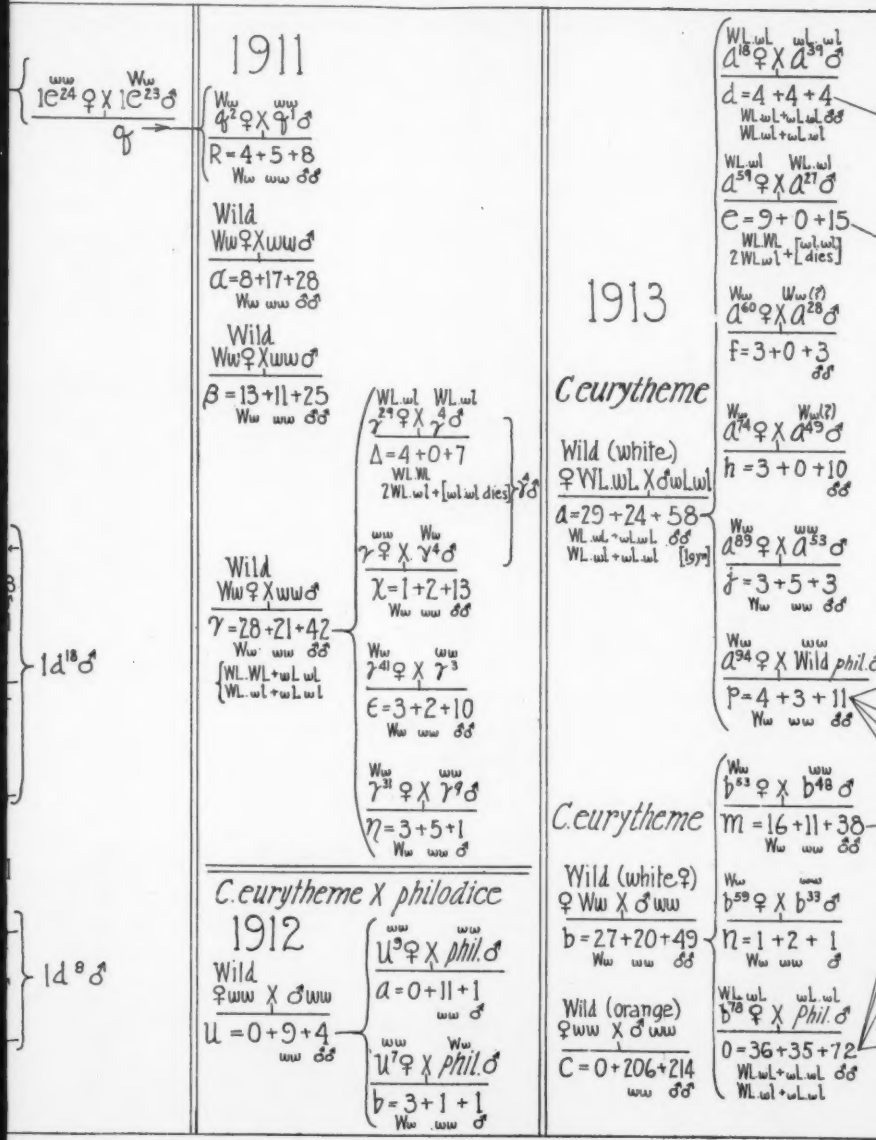
Wild
♀Ww X ♂ ww
b = 22 + 28 + 79
Ww ww ♂♂

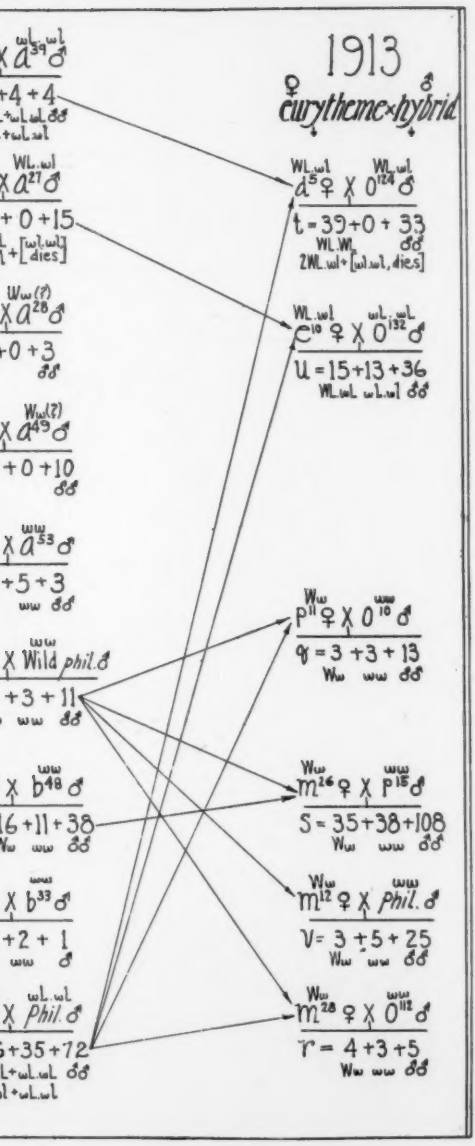
- Ww ww
  4b²¹ ♀ X 4b¹⁵ ♂
  m = 5 + 3 + 9
  Ww ww ♂♂
- Ww ww
  1b³⁹ ♀ X 1b³¹ ♂
  0 = 3 + 4 + 9
  Ww ww ♂♂

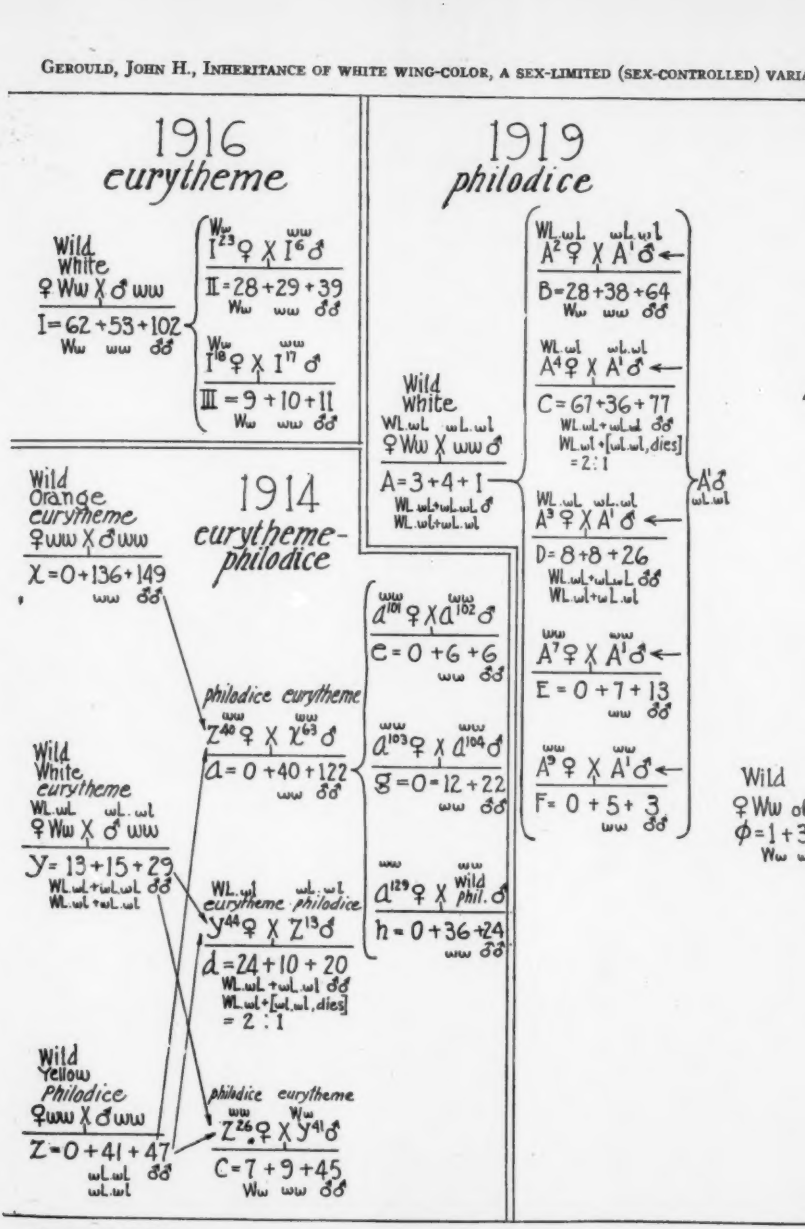
Wild
♀ww X ♂ Ww
c = 8 + 8 + 24
Ww ww ♂♂

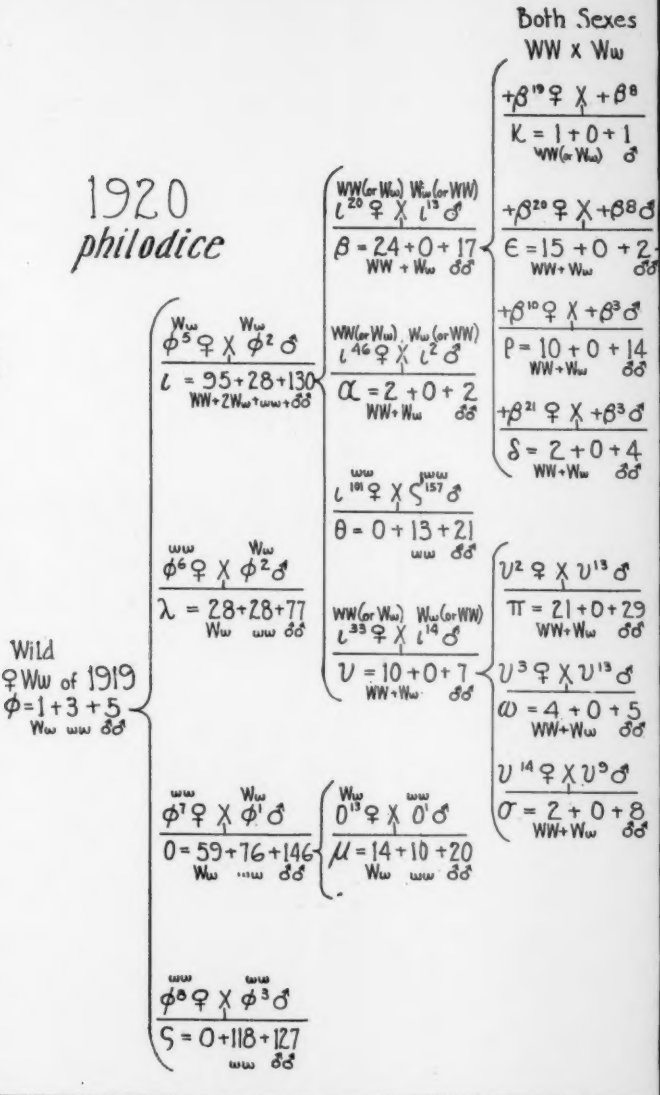
Wild
♀WL.wL X ♂wL.wl
d = 15 + 13 + 30
WL.wL + wL.wL ♂♂
WL.wl + wL.wl

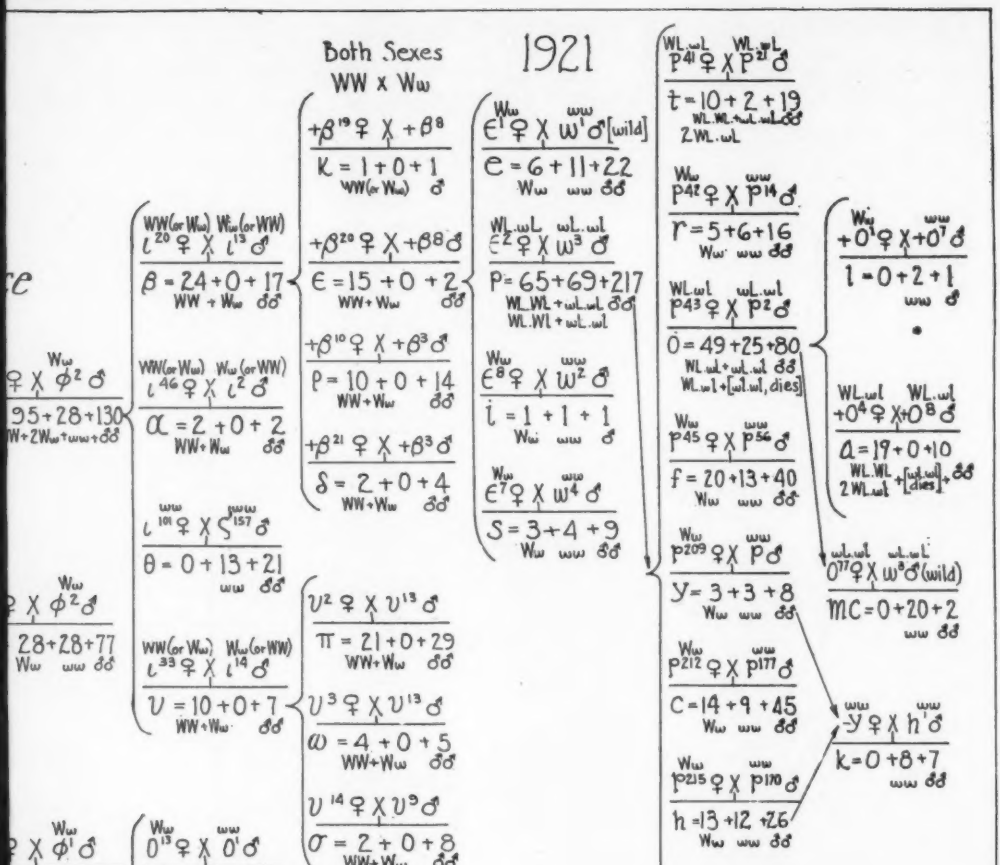
- Wl.wL WL.wl
  1d³⁵ ♀ X 1d¹⁸ ♂ ←
  g = 38 + 22 + 63
  WL.Wl + wL.wl ♂♂
  WL.wL + [Wl.wl, dies]
- Wl.wL WL.wl
  1d⁴⁵ ♀ X 1d¹⁸ ♂ ←
  h = 13 + 8 + 23
  (as in g) ♂♂
  → 1d¹⁸ ♂
- wL.wl WL.wl
  1d⁴⁶ ♀ X 1d¹⁸ ♂ ←
  l = 30 + 14 + 27
  WL.wL + wLwl ♂♂
  WL.wl + [wLwl, dies]
- wL.wL WL.wl
  1d³⁰ ♀ X 1d⁸ ♂ ←
  K = 19 + 19 + 46
  WL.wL wL.wl ♂♂
- Wl.wL WL.wl
  1d³⁶ ♀ X 1d⁸ ♂ ←
  → 1d⁸ ♂
  l = 3 + 3 + 4
  WL.Wl + wL.wl
  WL.wL + [Wl.wl, dies]


1911
1912
1913
C. eurytheme
C. eurytheme X philodice
Wild (white)
Wild (white?)
Wild (orange)
Wild
1d18♂
1d8♂


1913
♀ eurytheme×hybrid ♂
WL.wl WL.wl
d5 ♀ X 0124 ♂
t = 39+0+33
WL.Wl ♂♂
2WL.wl+[wl.wl, dies]
WL.wl wL.wL
c10 ♀ X 0132 ♂
u = 15+13+36
WL.wL wL.wl ♂♂
Ww Ww
P11 ♀ X 010 ♂
q = 3+3+13
Ww ww ♂♂
Ww ww
m26 ♀ X P15 ♂
S = 35+38+108
Ww ww ♂♂
Ww ww
m12 ♀ X phil. ♂
V = 3+5+25
Ww ww ♂♂
Ww ww
m28 ♀ X 0112 ♂
r = 4+3+5
Ww ww ♂♂


1916
eurytheme
Wild
White
♀ Ww X ♂ ww
I = 62 + 53 + 102
Ww ww ♂♂
I 23 ♀ X I 6 ♂
II = 28 + 29 + 39
Ww ww ♂♂
I 18 ♀ X I 17 ♂
III = 9 + 10 + 11
Ww ww ♂♂
1919
philodice
Wild
White
WL.wL wL.wl
♀ Ww X ww ♂
A = 3 + 4 + 1
WL.wL + wL.wL ♂
WL.wl + wL.wl
A2 ♀ X A1 ♂
B = 28 + 38 + 64
Ww ww ♂♂
A4 ♀ X A1 ♂
C = 67 + 36 + 77
WL.wL + wL.wL ♂♂
WL.wl + [wL.wl, dies]
= 2 : 1
A3 ♀ X A1 ♂
D = 8 + 8 + 26
WL.wL + wL.wL ♂♂
WL.wl + wL.wl
A7 ♀ X A1 ♂
E = 0 + 7 + 13
ww ♂♂
A9 ♀ X A1 ♂
F = 0 + 5 + 3
ww ♂♂
A1 ♂
wL.wl
1914
eurytheme-
philodice
Wild
Orange
eurytheme
♀ ww X ♂ ww
X = 0 + 136 + 149
ww ♂♂
philodice eurytheme
Z40 ♀ X X63 ♂
a = 0 + 40 + 122
ww ♂♂
Wild
White
eurytheme
WL.wL wL.wl
♀ Ww X ♂ ww
Y = 13 + 15 + 29
WL.wL + wL.wL ♂♂
WL.wl + wL.wl
WL.wl wL.wl
eurytheme philodice
Y44 ♀ X Z13 ♂
d = 24 + 10 + 20
WL.wL + wL.wl ♂♂
WL.wl + [wL.wl, dies]
= 2 : 1
Wild
Yellow
Philodice
♀ ww X ♂ ww
Z = 0 + 41 + 47
wL.wl ♂♂
wL.wl
philodice eurytheme
Z26 ♀ X Y41 ♂
c = 7 + 9 + 45
Ww ww ♂♂
a101 ♀ X a102 ♂
c = 0 + 6 + 6
ww ♂♂
a103 ♀ X a104 ♂
g = 0 + 12 + 22
ww ♂♂
a129 ♀ X Wild phil. ♂
h = 0 + 36 + 24
ww ♂♂
Wild
♀ Ww
♂ = 1 +
Ww


1920
philodice
Wild
♀Ww of 1919
φ=1+3+5
Ww ww ♂♂
Ww Ww
φ5 ♀ X φ2 ♂
ι = 95+28+130
WW+2Ww+ww+♂♂
ww Ww
φ6 ♀ X φ2 ♂
λ = 28+28+77
Ww ww ♂♂
ww ww
φ7 ♀ X φ1 ♂
0 = 59+76+146
Ww ww ♂♂
ww ww
φ8 ♀ X φ3 ♂
ς = 0+118+127
ww ♂♂
WW(or Ww) Ww(or WW)
ι20 ♀ X ι13 ♂
β = 24+0+17
WW + Ww ♂♂
WW(or Ww) Ww(or WW)
ι46 ♀ X ι2 ♂
α = 2+0+2
WW+Ww ♂♂
ww ww
ι101 ♀ X ς157 ♂
θ = 0+13+21
ww ♂♂
WW(or Ww) Ww(or WW)
ι33 ♀ X ι14 ♂
υ = 10+0+7
WW+Ww ♂♂
Ww ww
0 13 ♀ X 0 1 ♂
μ = 14+10+20
Ww ww ♂♂
Both Sexes
WW x Ww
+β19 ♀ X +β8
κ = 1+0+1
WW(or Ww) ♂
+β20 ♀ X +β8 ♂
ε = 15+0+2
WW+Ww ♂♂
+β10 ♀ X +β3 ♂
ρ = 10+0+14
WW+Ww ♂♂
+β21 ♀ X +β3 ♂
δ = 2+0+4
WW+Ww ♂♂
υ2 ♀ X υ13 ♂
π = 21+0+29
WW+Ww ♂♂
υ3 ♀ X υ13 ♂
ω = 4+0+5
WW+Ww ♂♂
υ14 ♀ X υ5 ♂
σ = 2+0+8
WW+Ww ♂♂


1921
Both Sexes
WW x Ww

yellow, daughters. Half of the expected yellow females failed to appear. It may be worth noting in passing that both of these unusual broods showed also a marked shortage of males.[4]

The reciprocal cross to this, a homozygous yellow female × a male heterozygous for white female coloration, produced in 1910 30 white daughters and 14 yellow daughters, 2 : 1 instead of 1 : 1 (1910, i, table 6, *D*).

In explanation it may be assumed that both parents in each case were heterozygous for a lethal factor closely linked with yellow, which destroyed one quarter of the offspring, namely, one-half of the expected recessives. Two of the three fraternities under consideration are from brother-sister matings favorable for bringing to light any recessive lethal factors that might be latent.

The explanation as applied to the case of 1919 C works out as follows: The mother, A[4]♀, may be supposed to have the constitution *WL. wl*, heterozygous for white-yellow and for the lethal factor, *Ll*, but with the lethal factor, *l*, linked with yellow (*w*). The mate would then be *wL. wl*, and the resulting offspring: *WL.wL* (white), *WL.wl* (white), *wL.wl* (yellow), *wl.wl* (dies), of which the last would be eliminated by the lethal factor, leaving two types of white, one normal, one heterozygous for the lethal factor, to one surviving yellow, heterozygous for the lethal. In 1910, i, the recessive yellow mother, *wL.wl*, mating with a male heterozygous for white and for the yellow-linked lethal factor, i. e., *WL.wl*, produced: *WL.wL* (white) + *WL.wl* (white) + *wL.wl* (yellow) + *wl.wl* (dies), or 2 white daughters : 1 yellow daughter.

Analysis of the four generations of *C. philodice* that came to maturity in 1920, as already stated, leads to the conclusion that in this strain lethal factors were not present and *WW* is viable. ϕ^2♂, mated with the recessive yellow sister ϕ^6, gave 28 white daughters and 28 yellow daughters, and was clearly heterozygous for white. Mated again with a heterozygous white sister, ϕ^5, a perfectly definite 3 : 1 ratio (95 : 28) was obtained, which has already been discussed.

[4] 1919, C(103 ♀♀, 77 ♂♂) lacked about 25 percent of the normally expected males, which should be 105+. It is conceivable that the missing males were non-viable heterozygotes for the same lethal factor that in homozygous combination caused the shortage of yellow females and eliminated a corresponding number of males. This assumption is supported by 1910, i, which had 44 ♀♀ and only 27 ♂♂, lacking about 40 percent of normally expected males, and 1910, l, in which a similar shortage occurred. In the hybrid cross 1914, d, = 34 ♀♀, 20 ♂♂, likewise over 40 percent of the expected males were missing. There was a similar shortage of ♂♂ in the hybrid families of 1913, d, and t, in which a lethal was evident (17+ percent of ♂♂ missing in t), but on the other hand a normal excess of males occurred in 1913, e, and the families of 1921 in which the yellow-linked lethal crops out (t, o, d).

This makes it evident that homozygous white females and males corresponding to them (*WW*) do occur, and, mated together or with heterozygous (*Ww*) males, should give all-white broods. 1921 β, α, and υ, are such broods. β inbred and υ inbred gave a generation of seven families, every one of which was all-white. There is no evidence that this strain contained any yellow-linked or white-linked lethal factors. The seven families (κ to σ) of the fourth 1921 generation consisted of *WW*+*Ww* or *WW*+*WW* combinations of females and males.

As previously stated, the only individuals of this strain that hibernated and produced broods (e, p, i, s) in 1921, were heterozygous females, for, mated with wild males from Annandale-on-Hudson, they produced in every case equal numbers of heterozygous white and recessive yellow daughters. This proved not only that the wild males were recessives, *ww*, but that all of the tested females of the all-white strain were *Ww*.

That we had been dealing only with *Ww* individuals in the two generations of all-white-female families and that *WW* is always lethal, as I assumed in my earlier paper, I do not regard as probable, in view of the large numbers in the conspicuously 3 : 1 ratio of 1921, and yet I would not dogmatically assume that the whole case is not one of balanced lethals. I have not yet proved to my entire satisfaction that some females of an all-white strain are homozygous.

Into this all-white strain there was introduced heterozygously by the wild *ww* male from Annandale two recessive factors, one for the olive-green caterpillar and butterfly color described in other papers, and one for a yellow-linked lethal. This male, in other words, was heterozygous for olive-green *Oo* [normal for the recessive blue-green carried by his white-winged mate, i.e., *BB*] and heterozygous for the yellow-linked lethal, *wL.wl*. Since the white female mate, ϵ^2, was normal for both of these factors, *OO*, grass-green, and *WL.wL*, white [heterozygous for blue-green, *Bb*], their immediate progeny, 1921 p, were phenotypically normal, but consisted of an equal mixture of heterozygotes for blue-green and olive caterpillar color and their normal allelomorphs, equal numbers of whites normal and whites heterozygous for yellow-linked lethal, of yellows normal and yellows heterozygous for yellow-linked lethal.

The mating is as follows:

$$1921\epsilon^2\,♀ \times w^3♂, \text{ i.e., } ♀\ WL.wL\,[Bb]\,OO \times ♂ wL.wl\,[BB]\,Oo$$

From this mating came 1921, p, consisting of 65 heterozygous white and 69 recessive yellow females. That they were in equal numbers heterozygotes and normals for recessive caterpillar variations does not concern us here, save to say in passing that in the next following generation (1921, t to d), some of the nine fraternities of caterpillars were all grass-green;

some were 9 grass-green : 3 olive : 4 blue-green; others 3 grass-green : 1 olive; still others 3 grass-green : 1 blue-green.

Two of the adult broods of this generation brought to light the recessive lethal factor linked to yellow, namely, 1921, o, consisting of 49 white females, 25 yellow females (and 80 males) and d, containing, in spite of the fact that neither of the parents could have been homozygous for white, white female offspring exclusively, namely, 28 white females and 30 males. From family o, a mating was made ($+o^4♀ \times +o^8♂$) which likewise produced a brood containing (19) white females only, 1921, a.

The clear-cut 2 : 1 ratio in family 1921, o, was obtained from a white mother ($p^{43}♀$) that must have been heterozygous for white, *Ww*, since she belonged to a family of heterozygotes and recessives in equal numbers, 65 : 69. If her mate ($p^2♂$) was *ww* and like herself heterozygous for a lethal factor linked with yellow, *wl* (i.e., ♀ *WL.wl* × ♂ *wL.wl*), a half of their homozygous yellow offspring would have been eliminated, namely, those homozygous for the lethal factor, giving 2 white : 1 yellow, which was actually the case (49 white ♀♀, 25 yellow ♀♀). If, on the other hand, the male had been heterozygous for both *w* and *l* (*WL.wl*), they would have produced white daughters only, as in 1921, d and a, or the 2 : 1 ratio that was actually realized could have been produced if the male had been not *ww* but *Ww*, and if in one of the mates the lethal factor had crossed over from *w* to *W*, as in 1910 g and h.

The parent family and the two following generations are shown in the following scheme:

$$1921, \epsilon^2♀ \;(WL.wL) \times w^3♂ \;(wL.wl)$$

$$1921, \text{p} = \underset{\text{white}}{WL.wL} + \underset{\text{white}}{WL.wl} + \underset{\text{yellow}}{wL.wL} + \underset{\text{yellow}}{wL.wl}$$

$$p^{43}♀ \;(WL.wl) \times p^2♂ \;(wL.wl)$$

$$1921, \text{o} = \underset{\text{white}}{WL.wL} + \underset{\text{white}}{WL.wl} + \underset{\text{yellow}}{wL.wl} + \underset{\text{dies}}{[wl.wl.]}$$

$$= 49 \text{ white} ♀♀ + 25 \text{ yellow} ♀♀$$

$$p^{351}♀ \;(WL.wl \times p^{296}♂ \;(WL.wl)$$

$$\text{d} = \underset{\text{white}}{WL.WL} + \underset{\text{white}}{2WL.wl} + \underset{\text{dies}}{[wl.wl]}$$

$$= 28 \text{ white} ♀♀$$

$$+o^4♀ \;(WL.wl) \times +o^8♂ \;(WL.wl)$$

$$1921, \text{a} = \underset{\text{white}}{WL.WL} + \underset{\text{white}}{2WL.wl} + \underset{\text{dies}}{[wl.wl]}$$

$$= 19 \text{ white} ♀♀$$

Returning to family p, from which the nine matings were made, two of which provided the lethal combination (*ll*), we have assumed that it was made up of individuals of which half were heterozygous for the lethal factor, half were normal. The matings, therefore, should have occurred, if at random, as follows: 1 $LL \times LL$, 2 $LL \times Ll$, 1 $Ll \times Ll$ (the lethal combination). Thus a quarter of the nine matings, namely, 2.25, should have furnished the lethal combination, *ll*, as two, in fact, did.

The different results, 2 : 1 or 3 : 0, depend, it is clear, upon whether the male parent involved has a genetic constitution for female coloration like his mate, *Ww*, or is a homozygous recessive, *ww*.

Turning back to the anomalous family, 1913, t, females all white, of which neither parent could have been homozygous for white, since they came from unrelated families consisting of equal numbers of heterozygotes and recessives, we find a combination precisely like that in 1921, d and a.

One of the respective parents in each of the families of the previous generation (1913, d, and the species-hybrid family, o) presumably was heterozygous for the lethal factor, so that half of their offspring (d and o) were also. 1913, t, derived from $d^5 ♀ \times o^{124} ♂$ ($WL.wl \times WL.wl$) consisted of $WL.WL + 2\,WL.wl + [wl.wl] = 39$ white females and no yellow females (33 males).

In 1913, e, (*C. eurytheme*) consisting of 9 white females, no yellow females (15 males), we find a similar combination, though this is too small a family to exclude the possibility of the 3 : 1 tendency. No homozygous white females were present in the previous generation, 1913, a. There were 29 heterozygous white, 24 recessive yellow females in this family. They were inbred, giving (9) white females only. $WL.wl \times WL.wl$, as before, gave $WL.WL + 2\ WL.wl + [wl.wl]$ females, all white, assuming that the male parent was heterozygous for female whiteness. Possibly the small brood, 1911, Δ, consisting of 4 white and no yellow females, is of the same type.

In our retrogressive survey we have now reached the anomalous families of 1910, g, h, i, which I explained in my earlier paper on the assumption that the *WW* combination is lethal. This hypothesis, however, did not explain why family i from a recessive yellow mother consisted, like the two others, g and h, from a heterozygous mother, of 2 white daughters; 1 yellow daughter. With the assumption of a yellow-linked lethal, the group may now be explained.

The male parent, $1d^{18} ♂$, was heterozygous for female coloration. His offspring, i, from the yellow female $1d^{46} ♀$ show that (see table 6, *D*). He was mated with the two white females: $1d^{39}$, producing 1910, g, and

1d[45], giving 1910, h. The composition of brood 1910, i, from the yellow female is as follows:

$$1d^{46}\,♀ \times 2d^{18}\,♂$$
$$(wL.wl) \mid (WL.wl)$$
$$WL.wL + WL.wl + wL.wl + [wl.wl],$$
white white yellow dies

that is, two white females (one normal, one carrying the lethal gene) to one yellow female.

1910, g and h (from white females), consisting, respectively, of 38 : 22, 13 : 8, are explicable on the 2 : 1 basis by assuming a crossover in the female parents of the lethal gene from yellow, *w*, to white, with very close "coupling." In that case: $Wl.wL\,♀ \times WL.wl\,♂$, gives

$$WL.Wl + WL.wL + [Wl.wl] + wL.wl,$$
white white dies yellow

or two viable white females to one yellow. But, as crossing over in both mothers with complete linkage to white may be regarded as unlikely, we have the alternative of assuming that both these female parents were normal, *LL*, as regards the lethal factor. That would result in the 3 : 1 ratio. Thus, $WL.wL\,♀ \times WL.wl\,♂$, gives $WL.WL + WL.wL + WL.wl + wL.wl$ or 3 white females to 1 yellow female.

But the numbers 38 : 22 (and 62 males), 13 : 8 (and 23 males) approach the 2 : 1 ratio more nearly than 3 : 1.

Résumé

The irregular ratios discussed in this section may be explained by the assumption of a lethal gene closely linked with the factor for yellow female coloration. A similar lethal gene to that which occurs in *C. philodice* appears also in *C. eurytheme* and in the cross between the two species.

The hypothesis of a yellow-linked lethal explains why all-white families have repeatedly been produced by two heterozygous parents (belonging to broods made up of heterozygotes and recessives in equal numbers). It explains why 2 white : 1 yellow female offspring have been produced by a heterozygous white female mated to homozygous recessive for female coloration, and by a yellow female mated to a male heterozygous for white.

While the evidence in regard to the viability of the homozygous white combination is not wholly satisfactory, it seems probable that in certain strains homozygous white individuals actually occur.

A 7 : 9 ratio

It will be noticed that the regular 50 : 50 ratio from $♀ ww \times ♂ Ww$ in table 5 is considerably disturbed by the anomalous family 1920, o, of 59 white :

76 yellow females and 146 males. This is almost exactly a 7 : 9 ratio in a large brood. One-eighth of the females, (namely, of white, *Ww*, constitution) are missing. Lack of greenhouse space prevented a thorough investigation of this interesting strain, only a single pair (o^{13}♀ *Ww*×o^{1}♂ *ww*) from it being bred. The offspring (1920, $\mu = 14$♀♀*Ww*+10♀♀*ww*+20♂♂) showed no marked divergence from the 1 : 1 ratio. In the absence of further data, an attempt to explain this anomalous brood must be mere speculation. Possibly a gametic lethal destroyed one-fourth of the white-bearing eggs of the *Ww* mother (ϕ^{7}), giving an expectation of $57\frac{6}{7}$ white : 77_{7} yellow, against the actual 59 : 76.

STABILITY AND PROPORTIONS OF THE WHITE VARIETY IN THE GENERAL POPULATION

After the publication of my earlier paper I made an effort, by no means very thorough, to check up the statement that at Hanover, New Hampshire, "the proportion of white females to yellow is, perhaps, roughly 5 percent."

In 1911 I made in this same locality the following counts of captured females, allowing none to escape lest they be counted twice:

	White	*Yellow*
May 16,	2	3
" 17,	3	9
" 20,	5	18
" 30,	0	12
June 8	0	10
Total	10 white	52 yellow

or 19.2 percent white females in the population. In July and August, 1923, R. A. LATTIMORE, under my direction, caught at Hanover, New Hampshire, 37 yellow and 4 white females; i.e., 9.75 percent of females were white.

In southern New Hampshire (Goffstown, N. H., on August 21, 1917) I captured 2 white females and 50 yellow females; i.e., only 4 percent were white.

In my earlier paper I assumed that the absence of homozygous white individuals in the stock of *C. philodice* that I had then bred, was to be explained by the probably lethal effect of the homozygous white combination, similar to that which is characteristic of homozygous yellow mice. I did not deny altogether the existence of homozygous white stock, for it was well known that white males had been captured in certain localities where the white variety is abundant, and I assumed that these were probably homozygous males and that homozygous white females would

occur with them. This was consistent with the assumption that in the male yellow is dominant, white recessive.

Having finally bred stock which apparently included homozygous white females and in which the males all proved to be yellow, I have discarded the theory of reversal of dominance. White, I now assume, is the dominant color, but the epistatic wing colors of the male prevent in that sex the expression of the genes for female wing coloration.

The question now arises: What would be the effect upon a population having a hereditary character, either dominant or recessive, so completely lethal that it can never appear in homozygous combination,— a population in which the rare homozygous white female, for example, should never appear.

My colleague, Professor J. W. YOUNG, has proved mathematically that a population made up of homozygous recessives and of heterozygotes for a single pair of allelomorphs, mating among themselves entirely at random, if the homozygous dominant be absolutely non-viable, would eventually lose entirely the dominant factor and be composed merely of recessives. The same principle would hold, *per contra*, if the homozygous recessive were non-viable, (i.e., if a recessive lethal factor were inseparably linked with any recessive gene) the recessive factor in question in that case would eventually disappear.

This may appear at first sight unlikely, when one thinks of the maintenance of the stocks of yellow mice in which homozygous yellows are non-viable. By selective mating of yellow $\times$ yellow, or yellow $\times$ non-yellow, the yellow race can, of course, be maintained indefinitely, but if yellow mice should be set free in even a small population of non-yellow that are as likely to mate together as with heterozygous yellow individuals, the result eventually would be the extinction of the race of yellow mice.

Professor YOUNG'S computation proves that a case like that of yellow mice could not exist under natural conditions involving no selective processes, and demonstrates that my earlier assumption is incorrect that in the absence of selection, inherently lethal results attend the white-white combination.

It is as follows:

In a given population let aa and Aa individuals exist in proportions p and q, respectively, males and females of each type in equal numbers, such that $p+q=1$.

Random matings would occur in the following proportions, the first of each pair representing the female:

♀	♂		
aa	$\times aa$	give	p^2 (aa)
aa	$\times Aa$	give	$\frac{1}{2}\ pq(aa) + \frac{1}{2}pq\ (Aa)$
Aa	$\times aa$	give	$\frac{1}{2}\ pq(aa) + \frac{1}{2}\ pq\ (Aa)$
Aa	$\times Aa$	give	$\frac{1}{4}\ q^2\ (aa) + \frac{1}{2}\ q^2\ (Aa) + \frac{1}{4}q^2(AA$, lethal)

Collecting terms, this gives for the first generation:

$(p + \frac{1}{2}q)^2$ of aa
$q(p + \frac{1}{2}q)$ of Aa
$\frac{1}{4}q^2$ of AA, which die.

[As a check on this calculation, observe that the sum of these numbers is $(p+q)^2$, as it should be.]

aa and Aa then occur in the proportion:

$$p+\tfrac{1}{2}q : q$$

Since $p=1-q$, this ratio may be written:

$$1-\tfrac{1}{2}q : q$$

The proportion of Aa is then $\dfrac{q}{1+\frac{1}{2}q} = \dfrac{2q}{2+q}$ after the first mating, that is, for the first generation.

In the second generation the proportion of Aa individuals becomes $\dfrac{2}{2+2q}$; in the Kth generation, $\dfrac{2}{2+Kq}$.

With increasing K this number decreases indefinitely, so that the dominant character *A would ultimately die out.*

In the actual population of butterflies with which I have worked, Doctor YOUNG has shown mathematically, not only that the small proportion of dominant whites must be stable, provided no selective processes are at work, but also that starting with 5 percent of the population white (5 percent ♀♀, 5 percent white-latent ♂♂) the proportion of homozygous dominant white females in the first generation, and later, would amount to only 6.25 in ten thousand, as compared with 487.5 heterozygous white females in ten thousand, the remaining 9506.25 being yellow. Hence the exceeding rarity of homozygous white females in this locality. *Heterozygous white females*, assuming a 5 percent heterozygous white female population at the beginning, would be *78 times as common as homozygous*. If white females comprise 10 percent of the original female population, heterozygous white individuals are 38 times as abundant as the homozygous.

Doctor YOUNG's computation is as follows:

Let ww, Ww and WW individuals occur in the original population in the proportions p, q and r, respectively, and $p+q+r=1$, males and females of each type in equal numbers.

Random mating would produce crosses in the following proportions:

		♀♀ ♂♂
p^2	of	$ww \times ww$
q^2	of	$Ww \times Ww$
r^2	of	$WW \times WW$
pq	of	$ww \times Ww$
pq	of	$Ww \times ww$
pr	of	$ww \times WW$
pr	of	$WW \times ww$
rq	of	$Ww \times WW$
rq	of	$WW \times Ww$

These crosses would produce individuals of the various types as follows:

	ww	Ww	WW
$ww \times ww$	p^2		
$Ww \times Ww$	$\frac{1}{4}q^2$	$\frac{1}{2}q^2$	$\frac{1}{4}q^2$
$WW \times WW$			r^2
$ww \times Ww$	$\frac{1}{2}pq$	$\frac{1}{2}pq$	
$Ww \times ww$	$\frac{1}{2}pq$	$\frac{1}{2}pq$	
$ww \times WW$		pr	
$WW \times ww$		pr	
$Ww \times WW$		$\frac{1}{2}qr$	$\frac{1}{2}qr$
$WW \times Ww$		$\frac{1}{2}qr$	$\frac{1}{2}qr$
Total	$(p+\frac{1}{2}q)^2$	$2(p+\frac{1}{2}q)(\frac{1}{2}q+r)$	$(\frac{1}{2}q+r)^2$

Check: The sum of the three totals is $(p+q+r)$.[2]

We then have in F_1, ww, Ww and WW, occurring in the proportions p_1, q_1, and r_1, where

$$\left.\begin{aligned} p_1&=(p+\tfrac{1}{2}q)^2 \\ q_1&=2(p+\tfrac{1}{2}q)(\tfrac{1}{2}q+r) \\ r_1&=(\tfrac{1}{2}q+r)^2 \end{aligned}\right\} \quad p_1+q_1+r_1=1$$

Now place $q=1-p-r$, and substitute in p_1 and r_1:

$$p_1=(p+\tfrac{1}{2}-\tfrac{1}{2}p-\tfrac{1}{2}r)^2=\tfrac{1}{4}(1+p-r)^2$$
$$r_1=(\tfrac{1}{2}-\tfrac{1}{2}p-\tfrac{1}{2}r+r)^2=\tfrac{1}{4}(1-p+r)^2$$

Let $p-r=d$, then

$$q_1=\tfrac{1}{2}(1-d^2)$$

These results show that p_1, q_1, r_1 depend only on $d=p-r$.

The distribution in F_2, namely, p_2, q_2, r_2, would be obtained by similar calculations on $d_1 = p_1 - r_1$. But

$$d_1 = p_1 - r_1 = \left(\frac{1+d}{2}\right)^2 - \left(\frac{1-d}{2}\right)^2 = d$$

That is, $p_2 = p_1$, $q_2 = q_1$, $r_2 = r_1$, that is, *the population is stable after the first mating.*

The formulas for p_1, q_1, r_1 in terms of d show that

$4p_1r_1 = q_1^2$, or $r_1 = \frac{q_1^2}{4p_1}$, which shows that r_1 is very small if q_1 is small compared with p_1.

Numerical results:

Original population $p = .95$, $q = .05$, $r = 0$ gives for the stable population:

$$\begin{aligned} p_1 &= .950625 \\ q_1 &= .04875 \\ r_1 &= .000625 \\ \hline & 1.000000 \end{aligned}$$

Original population, $p = .9$, $q = .1$, $r = 0$, results in stable population:

$$\begin{aligned} p_1 &= .9025 \\ q_1 &= .095 \\ r_1 &= .0025 \\ \hline & 1.0000 \end{aligned}$$

d	p_1 $\frac{1}{4}(1+d)^2$	r_1 $\frac{1}{4}(1-d)^2$	q_1 $\frac{1}{2}(1-d^2)$		
.95	.950625	.000625	.04875	=	1.00000
.90	.9025	.0025	.09500	=	1.00000
.85	.855625	.005625	.13875	=	1.00000
.80	.8100	.0100	.18000	=	1.00000
.75	.765625	.015625	.21875	=	1.00000
.70	.7225	.0225	.25500	=	1.00000
.65	.680625	.030625	.28875	=	1.00000
.60	.6400	.0400	.32000	=	1.00000
.55	.600625	.050625	.34875	=	1.00000
.50	.5625	.0625	.37500	=	1.00000

JENNINGS (1916, page 65, paragraph 8) has given the following general formulae covering this case. If at the beginning of random mating the population consists of $r\,AA + s\,Aa + t\,aa$, then in any following generation:[4]

[4] I have made the corrections suggested by the author.

JENNINGS		YOUNG
$aa\ (=t) = (s+2t)^2$	=	$p_1 = (p + \frac{1}{2}q)^2$
$Aa\ (=s) = 2(s+2r)(s+2t)$	=	$q_1 = 2(p + \frac{1}{2}q)(\frac{1}{2}q + r)$
$AA\ (=r) = (s+2r)^2$	=	$r_1 = (\frac{1}{2}q + r)^2$

By comparison of the two sets of formulae worked out by JENNINGS and by YOUNG it will be seen that they essentially correspond.

What bearing, if any, does the disturbance in ratios observed in these experiments in inbreeding have upon the proportions of white to yellow in the general population? I am of the opinion that the continual outcrossing that takes place in butterflies flying in the fields, generally covers up the recessive lethal factor closely linked with yellow, so that the lethal, though producing irregularities, does not materially affect the proportions of white to yellow. The computations made by Doctor YOUNG, therefore, are not invalidated by the lethal factor.

Twelve samples of wild broods of *C. philodice* and four of *C. eurytheme* are reassembled in the following list.

	C. philodice			*C. eurytheme*			
	Ww	*ww*	♂♂	*Ww*	*ww*	♂♂	
1908	2	3	3				
1909 1a	7	16	39				
1c	3	7	13				
1910 a	6	9	18				
b	22	28	79				
c	8	8	24				
d	15	13	30				
1911 α	8	17	28				
β	13	11	25				
γ	28	21	42				
1919 A	3	4	1				
1920 φ	1	3	5				
Total	116	140	307				
1913 a				29	24	57+1	gynandro-
b				27	20	49	morph
1914 y				13	15	29	
1916 I				62	53	109	
Total				131	112	244	

It is evident that in *C. philodice* there is a shortage of white (116 white, 140 yellow); in *C. eurytheme* a shortage of yellow (131 white, 112 yellow). Hybrids between them (see table 1) show an even balance (100 : 100).

Of the twelve broods of *C. philodice*, white is deficient in eight, yellow in only three, which certainly is no indication of disturbance in the general population by a yellow-linked lethal.

Two of the eight broods showing a minority of white females, approach a 2 : 1 ratio, namely, 1909, 1a = 7 white : 16 yellow, and 1911, a = 8 white : 17 yellow, suggesting that both parents might have been heterozygous for a white-linked lethal, but the numbers are small and the nature of the strains was not analysed by further breeding, except in one case which disclosed no lethal disturbance.

The data as a whole indicates that in *C. philodice* white is a little less viable, in *C. eurytheme* a little more viable, though it is uncertain whether the strains with which I have worked fairly represent the whole species to which they respectively belong.

BREEDING EXPERIMENTS WITH OTHER SPECIES OF COLIAS

Colias christina Edw.

Colias christina of southwestern British America and the northwestern United States immediately east of the Rocky Mountains, presents the most bewildering variety of colors of any American stock of this highly variable genus. Whether or not, as seems to me probable, this species is a hybrid between the widely distributed orange *Colias eurytheme*, and a sub-arctic, yellow, univoltine species with white female, like *C. pelidne* or *C. scudderi*, breeding experiments carried on by Mr. THOMAS E. BEAN at Laggan, Alberta, in 1891, prove that *C. christina* is a complex heterozygote for factors that determine the ground color (orange in different degrees of intensity, *versus* clear yellow, in both sexes; orange, or yellow, *versus* white, in the female). Variations in the color pattern of the female range from a broad black border, as in *C. eurytheme*, to none at all or the merest vestige of one, as in *C. pelidne* and *C. scudderi*.

The unpublished results of Mr. BEAN'S investigations, as shown in his notes upon seventeen families from lots of eggs from wild females of 1890 that with remarkable skill he brought through the winter into the adult stage (June 29 to July 15, 1891), are of great interest to students of genetics. With Mr. BEAN'S permission I wish to call the reader's attention here to the phase of this work that falls within the scope of the present paper, namely, the inheritance of the factor for whiteness in the female, which is shown in table 7 compiled from his notes.

It will be seen that the white females are uniformly heterozygous, producing equal numbers of heterozygous white and recessive yellow daughters.

Recessive yellow mothers are equally likely, according to these data, to breed true to yellow (the male in this case being homozygous for yellow), or to produce white and yellow daughters in equal numbers (the male in

the latter case being, presumably, heterozygous for white-yellow female coloration).

In only one family, 13, which I have accordingly omitted from the table, is there apparently any difficulty in classifying mother and daughters

TABLE 7

Female offspring of Colias christina bred by MR. THOMAS E. BEAN *at Laggan, Alberta.*

MOTHER	DESIGNATION OF BROOD	WHITE FEMALES	YELLOW FEMALES
White	3	10	10
	5	14	7
	6	7	3
	8	1	2
	17	2	3
Total		34	25
Yellow	1	7	4
	7	2	2
	9	2	7
	10	2	6
	11	7	5
Total		20	24
Yellow	12		5
	14		5
	15		4
	16		5
	18		3
Total			22

as white or non-white. The mother is described in the notes as "pale brownish-white with a yellow element." Her daughters are described as:

Greenish white	2
Milk white	1
Nearly white	2
Pale brown-white without yellow	1
Pale brown-white with yellow, "buff"	9
Yellow	1
	16

In this family No. 13 we probably have the result of interaction betweee more than one pair of factors, producing a series of intermediates between the clear white and yellow. In only one species of Colias that I havn examined have I found such a tendency toward continuity between white

and yellow wing color, namely, *Colias interior*. In *C. philodice* and *C. eurytheme*, though the white is in many cases suffused with yellow, due probably to secondary hereditary factors that control this yellow flush, the break between white and non-white is almost without exception abrupt.

Colias myrmidone Esp.

The breeding experiments of PIESZCZEK (1917) and his associates on the *alba* variety of *C. myrmidone* of Central Europe, which much resembles in normal coloration and its variations our *C. eurytheme*, show that homozygous white females occur in the mountainous regions of Upper Styria. Here a majority of the females in certain localities are white. *Alba*, however, is rare in the Austrian lowlands north of Styria (including spurs of the Austrian Alps and the region of Vienna), and nearly or quite lacking in the *myrmidone* population further north and west, i.e., Bavaria (Regensburg, on the Danube), Bohemia, Moravia (Brünn).

Homozygous as well as heterozygous whites have been shown to occur in the southern, mountainous part of the range of the species; heterozygous whites occur in the lower altitudes of the same region (near Graz), from which no homozygous whites are on record. Passing northward into the valley of the Danube, the heterozygous *alba* becomes rarer, and finally is exceedingly rare or disappears entirely from the *myrmidone* population on the great plains of Bohemia, Moravia, and the upper Danube.

Alba females from the mountainous parts of Upper Styria (Zeltweg and Gleisdorf) gave:

(6th culture): 7♂♂, 11♀♀, all *alba*,
(11th culture): 19♂♂, 19♀♀, all *alba*,

while a heterozygous white from the same region gave

(17th culture): 28♂♂, 18♀♀ *alba*, 17♀♀ red.

At lower altitudes near Graz, *alba* is rarer, but a sample of the population taken in the field by Dr. ZWEIGELT showed 22 percent of *alba* females (33 red♀♀, 7 yellow or "intermediate"♀♀, 11 *alba* ♀♀). The following broods raised by PIESZCZEK from *alba*♀♀ from this region prove that there the white females are commonly heterozygous. No broods from homozygous white females are, in fact, recorded.

(7th culture):	6♂♂, 1 white♀,	4 red♀♀
(10th culture):	14♂♂, 9 white♀♀,	5 red♀♀
(12th culture):	5♂♂, 7 white♀♀,	1 red♀
(13th culture):	5♂♂, 4 white♀♀,	5 red♀♀
(18th culture):	10♂♂, 2 white♀♀,	4 red♀♀
	23 white♀♀,	19 red♀♀

Several all-red broods from red females of the Graz region are described, and one lot from several red females from the mountains (Zeltweg, 16th culture) was evidently a mixture of the progeny from different mothers, one of which had mated with a male heterozygous for white, others with males homozygous from non-white (yellow). This mixed lot contained 67♂♂, 10 white♀♀, 42 cadmium (dark) yellow♀♀. It is beyond the scope of the present paper to discuss the inheritance of yellow *versus* orange, but interesting to note that a yellow (non-red) variety of *C. myrmidone* (ab. *schwabi*) occurs which is comparable to *C. eurytheme eriphyle* of the northwestern United States and British Columbia. Yellow females in the mountains of Styria are said to stand next to the white in numbers, and a remarkable intermediate between white and yellow is sometimes found (ab. *pieszczeki*).

WHITE WING COLOR AND CLIMATE

SCUDDER (1889) says in regard to the white variety in *Colias philodice*:

"In the north this rarely, almost never, occurs in the first brood of the season, and is found much more abundantly in the latest than in the middle brood, the numbers increasing as the season advances. In the south, however, if we may follow EDWARDS, it occurs not infrequently in the spring brood, but . . . it is not impossible that the same rule holds in the south as in the north."

This erroneous opinion of SCUDDER that the white female is nearly or quite limited to the second and third broods of the season is an illusion probably explained by the fact that butterflies of the spring brood in this species are much less abundant than those of the two later broods. Hibernating, as the species does, in the caterpillar stage, and unable to withstand a temperature much below freezing, the winter mortality is enormous, and, after an open winter when the roots of the grass among which the hibernating caterpillars rest are unprotected for long periods by any covering of snow, the spring brood is so reduced in numbers as to be noticeably rare. In the spring of 1916, for example, I saw no wild *C. philodice* at all until May 21, when one male was observed, and thereafter occasionally one or two males, until June 2, when the first female was seen, the species not becoming abundant until the third brood appeared. When one recalls that white females comprise only a very small proportion of the female population, it is of course evident that in a season like the one mentioned, females of the rarer variety might not be observed at all in the spring, but would be more and more in evidence as the species increases in abundance in the summer and autumn broods.

A few observations bearing upon this point taken from my field notes may be of interest. In 1911 three caterpillars (of known parentage) had sur-

vived the winter at the roots of white clover plants covered with a box upon a lawn, were found alive on April 27 and pupated May 5 and 6. All of the numerous other caterpillars protected by boxes upon the same lawn failed to survive, and the surrounding clover unprotected by boxes was winter-killed. On May 17 one white female and one male emerged from these chrysalids.

Wild males, however, appeared in the fields on May 8, and were abundant on May 14. About a hundred were seen on May 16 and with them five females, two white, three yellow. On May 17 three white and nine yellow females were caught, the former being kept for breeding.

1912. *Colias philodice* first appeared on May 26. On May 27, one white female and two males were caught and a few other males were seen.

1913. *Colias philodice* appeared on May 30. On June 2, not yet abundant, but three yellow females were caught; four more yellow females on June 4, one white female on June 5.

The spring brood was abundant in 1914, rare in 1915 and 1916. The first males in 1914 were seen May 16, in 1916 on May 21, in 1921 on May 9.

These notes corroborate my earlier observations that white females do occur in the spring brood and that this generation is reduced to rarity in this cold climate after certain winters.

W. H. EDWARDS (1882) refuted SCUDDER'S erroneous statement quoting from his own great work on the Butterflies of North America, volume 2 in regard to *C. eurytheme* as follows:

> "Albinic females appear in every brood, as in *philodice*. In that species (*philodice*) these females are as common in the early spring brood as in any of the later ones; and judging by the number of albinos received by me from many quarters, the same is true of *eurytheme*."

And he adds evidence showing that "albinic females do appear in the early spring brood, in New York as well as in West Virginia."

No evidence has come to my attention that altitude and climate have any direct or indirect effect upon the distribution of the white female variety in either *C. philodice* or *C. eurytheme*, comparable to that which has been described in the previous chapter for *C. myrmidone*. The white female variety of the last-mentioned species outnumbers the non-white in the Austrian Alps, but is rare or absent in the Austrian lowlands. This fact suggests that in *C. myrmidone*, climate, either indirectly through natural selection or, less probably, by direct action, controls the relative proportions of the two female varieties in the respective populations. STANDFUSS (1913) makes the statement that in his experiments on the

direct effect of cold upon pupae exposed to low temperatures at the critical period for the modification of wing pigments:

"Kälte gestaltete *Colias myrmidone* Esp. in einem erheblichen Bruchtheil der weiblichen Individuen zu Ab. *alba* Stgr. um, während das Orange der Männchen nach Gelb hin abgestumft wurde."

But no detailed account of this experiment is given stating that any control cultures were bred for comparison or that he knew anything about the genetics of the stock he was breeding, so we may well doubt whether exposure to cold had anything to do with the occurrence of a considerable proportion of white individuals among the females emerging from the pupae which he employed. That the orange of the males was reduced somewhat toward yellow seems, in the light of my experience with *C. eurytheme*, more probable, though not certainly demonstrated.

It would be of great interest to get more information in regard to the climatic effects upon this and other variations in wing color in this genus. Arctic species like *C. pelidne* and *C. scudderi* of British America have white females only, while *C. interior*, a subarctic species distributed in northern Canada from the Rocky Mountains and the northern shores of Lake Superior eastward to the Atlantic, has both types of female, though the white appears on the whole, according to SCUDDER, to be the more common. Two females of this species caught at the southern limit of their range in the New Hampshire mountains (Moosilauke) on July 25, 1921, were intermediate in color between white and yellow, unlike *philodice*, in which the difference between the two varieties of females is clear-cut.

The typical female of *C. palaeno* of Northern Europe is white, but in the Alps yellow varieties occur. In this species the yellow-white reaction in the wing pigments appears to depend much upon climate, for in Lapland even the male is white, and yellow, so far as I am aware, never occurs in that locality in either sex. In Germany and Northern Switzerland, the intermediate part of its range, the female is white and the male yellow, while in the Southern part of the Alps (Southward from the Simplon), according to PRELL (1915), only the yellow females occur. STANDFUSS (1913), furthermore, has found that in *Rhodocera* (*Gonepteryx*) *rhamni* L., in which the male is bright yellow, the female white, male wing color may be modified slightly by cold into a paler color, whereas the white color of the female may be more markedly transformed by high temperatures into yellow.

That cold has a similar inhibiting effect and heat a stimulating effect upon the development of yellow wing pigment in *C. philodice* has often been demonstrated in my cultures, but it is very slight as compared with

the promotion of the development of orange-red in *C. eurytheme* by heat, and of melanic pigment in both species by cold. The hereditary factor that determines white or yellow pigmentation in the females of these two species, however, is far more effective than heat or cold, the effects of which are comparatively slight and fluctuating.

COMPARISONS WITH PAPILIO

As my work on inheritance of the two female varieties in Colias progressed, resemblances became more and more evident between this case and that of two tropical species of Papilio which have respectively three forms of female. These are *Papilio memnon*, bred by JACOBSON (1909), and discussed from the point of view of genetics by DE MEIJERE (1910), and *P. polytes*, which has been somewhat more fully investigated by PUNNETT (1910, 1915) and FREYER (1914).

These resemblances are briefly three: (1) there is only one variety of male, but each male carries the genes for one of the two, or three, types of female; (2) one of the types of female roughly corresponds in ground color to the male, and may be called for convenience the male-like form. This in every case is a simple Mendelian recessive to the other one or two female types; (3) The dominant female types are alleged "mimics" of other species in their own genus (Papilio), while the dominant type in Colias shows a superficial resemblance to other (white) Pierids, and in the field may easily be mistaken for them. The inference is that resemblances are due to comparable genetic factors acting upon similar pigments with somewhat similar results, and that these particular cases of mimicry or pseudo-mimicry have no particular selective or protective value.

Discussing each of the points noted above we may turn (1) to the conclusion that there is in Colias only one type of male. In my earlier paper (GEROULD 1911) I brought out the fact, well known to entomologists, that white males exist, and I then assumed that they correspond to the homozygous white females, which I had not at that time bred and which I regarded as usually non-viable. Hence, I believed that white should be regarded as recessive in the male, yellow as dominant, the reverse of the situation in the female. More recently I succeeded in breeding for several generations stock probably containing homozygous white females, and found that males homozygous for white female coloration are yellow. GOLDSCHMIDT (1912), accordingly, was right when he held that white males should be produced only by a mutation that is entirely independent of the genes that determine the coloration of the female.

(2) The male-like type of female in *P. polytes* differs from the male in ground color by being slightly less intensely melanic. In Colias likewise the yellow ground color of the female is slightly less intense. The color *pattern* of the male and male-like type of female in *P. polytes* is practically identical; in Colias, while the color patterns of male and female are quite different, the dimorphic females have the same color pattern and differ from each other only in ground color. In *P. memnon* the recessive male-like female is highly variable and not closely male-like,

TABLE 8

Polymorphic females of Papilio and Colias.

SPECIES	DOUBLE-DOMINANT VARIETY	SINGLE-DOMINANT VARIETY	MALE-LIKE RECESSIVE VARIETY
Papilio memnon	var. *achates* ("mimic" of *coon*?)	*agenor*	*laomedon*
P. polytes	var. *romulus* ("mimic" of *P. hector*)	*polytes* ("mimic" of *P. aristolochiae*)	*cyrus*
Colias philodice	———	*pallidice* (white),	yellow
C. eurytheme	———	*alba* (pseudo-mimics of *Pieris rapae* and *P. oleracea*)	orange
Types of Papilio	*AABB* *AABb* *AaBB* *AaBb*	*AAbb* *Aabb*	*aaBB* *aaBb* *aabb*
Types of Colias	———	*AA* *Aa*	*aa*

being less intensely melanic and showing a spotted pattern which in males is nearly, or, in some individuals, quite obscured by the deeply melanic pigmentation. In all three species under consideration, however, the most male-like variety of female is recessive to other female types.

(3) The dominant female types of *Papilio polytes* are regarded as mimics of other Papilios in the same general regions in Asia, supposedly protected from the attacks of birds because their larvae feed on a poisonous Aristolochia. The tailed double-dominant type of *memnon*, *achates*, was regarded by WALLACE as the mimic of *P. coon*. Whether or not the latter species is protected from the attacks of birds and is a genuine example of mimicry, which, DE MEIJERE states, has been opposed on good grounds, the resemblance doubtless exists. Further, a long series of field observations on Coliads has impressed the fact on my mind that the dominant white female variety is a most excellent mimic of *Pieris rapae*

and closely allied cabbage butterflies, though neither are regarded by anyone, so far as I know, as examples of "protective mimicry." We have here a case which follows to the letter WALLACE'S rules of protective mimicry except that it exists between "unprotected" species.

The conditions under which WALLACE claimed that mimicry occurs, are well met by the white female of *Colias philodice* except that no warning colors are involved, likeness to the white species of Pieris being due to essential identity in the chemical nature of the pigments, based on a common genetic origin. The supposed imitators occupy the same region as *Pieris rapae*; they "are always less numerous in individuals"; they "differ from the bulk of their allies"; and the imitation is superficial. The same facts are probably true of the white female of various species of Colias in various parts of the world, and yet, of course, no one appeals to natural selection to account for this striking case of resemblance. No good models for *P. memnon* have been discovered, and PUNNETT has shown how imperfect are the resemblances between the two dominant and probably primitive types in *P. polytes* on the one side and their two Aristolochia-feeding relatives that belong to another branch of the same genus.

Each case of "mimicry" should be studied by itself, for under this comprehensive term are included a vast array of resemblances among forms most diverse. Probably similarity of mutating genetic factors is not the only explanation that we need for these interesting phenomena, about the physico-chemical conditions, internal and external, under which they appear, we know so little, but for the mimicry theory to stand upon its feet its proponents should prove that "warning" colors warn to such an extent that for a near relative to lack them would be fatal, or at least lessen its chances of perpetuating its phenotype, a very difficult proposition indeed. I have been amused, while staying at the summit of Mt. Moosilauke (White Mountains, New Hampshire), in watching a finch, *Junco hiemalis*, feed on the swarms of "highly protected" wasp-like Syrphus flies that rested and sunned themselves in vast numbers on the rocks. Their fancied protection seems much more obvious than that ascribed to whole groups of butterflies.

The general conclusion is reached that a remarkable similarity obtains between these examples of inheritance of female polymorphism in Papilionidae and Pieridae, which have been established by a simple genetic process, namely by the appearance of mutations involving one or two pairs of Mendelian factors. There is no evidence that natural selection has had any definite selective influence in the origin of the varieties, or that mimicry has been involved.

If one may venture cautiously into the field of phylogenetic speculation, some fairly cogent reasons can be stated for regarding the dominant female types in both Colias and Papilio as possibly the more primitive. *Achates*, the double-dominant female of *P. memnon*, has wing-tails; the two types recessive to it (*agenor* and *laomedon*) lack them. Most modern Papilios have wing-tails, so that *agenor* and *laomedon* may be reasonably regarded as having sprung from *achates* by losing the wing-tails. It may be hazardous for one who is not an expert in this genus to assert that *achates* has also a generalized pattern, but I would call the reader's attention to the remarkable resemblance of the color pattern of *achates* to that of the double-dominant female variety in *polytes* (i.e., *romulus*). The black forewings suffused with gray and the central white spot upon the hind wings are striking features that they possess in common. Roughly, *achates* looks like a very much enlarged *romulus* lacking some of the reddish markings of the hind wings but having a dash of the same pigment on the shoulders. This suggests the possibility that the double-dominant pattern which *achates* and *romulus* have in common may be the most primitive of all these various types, and that the others may have arisen from it by the sudden appearance of recessive genes.

The white female of Colias likewise was regarded by STANDFUSS (1896) as more primitive than the yellow, since the ground color of many of the Pieridae is white, which is the color of the monotypic female in certain arctic species. STANDFUSS concluded that, from this white primary type, the male individuals of many species first became yellow, and were later followed by the females, in the evolutionary process, which in the main was saltatory.

> "Die Weibchen dieser Arten nahmen die gelbrote Grundfarbe wohl erheblich später als die männlichen individuen an und gingen mit grossen Sprung, indem eine gelbe Zwischenstufe, wie es scheint, ganz wegfiel, aus der weissen Form direkt in die orangefarbene über."

The exceptional white females of the yellow-red species, he concludes, are to be regarded as reversions to, or relics of, the more primitive female type. If this is true, and it seems to the present writer plausible, evolution has proceeded by the acquisition of recessive factors that change the uric acid derivatives (to which HOPKINS (1894) has found these pigments to be due) from white to yellow.

The results obtained from *P. memnon* and *P. polytes* differ in one important respect. In the former no type of female produced more than two kinds of female offspring, e.g., like itself and like one of the varieties recessive to itself. *P. polytes*, on the other hand, produced in

FREYER'S (1914) experiments nine broods containing examples of all three varieties, and this occurred in one case in which the female was of the recessive, male-like type but had evidently mated with a male heterozygous for the factors of both dominant forms. FREYER'S observations were more extensive than JACOBSON'S, and it is quite possible that more complete data on *P. memnon* may bring it into line with *P. polytes* in this respect.

DE MEIJERE (1910) proposed the following scheme for the genetic constitution for females of the three types in *P. memnon*:

Achates (dominant)	*Agenor*	*Laomedon* (male-like recessive)
Ach. Ach	*Ag. Ag*	*L.L*
Ach. Ag	*Ag. L*	
Ach. L		

GOLDSCHMIDT'S original modification of this scheme consisted in the substitution of G^2, G^1, G, for *Ach.*, *Ag.*, and *L.*, assuming a series of mutations in a *single pair* of factors representing the female coloration, namely, the recessive (male-like) pattern GG becoming G^1G^1, or G^2G^2, or heterozygous combinations of these factors. Moreover, the female was assumed to be always heterozygous for another factor representing the complex of male secondary sexual characters, A, namely, Aa, for which the male is always homozygous, AA. This factor he regarded as closely linked with the sex-determining factor (in the same chromosome) so as to be practically identical with it and, being epistatic to G in homozygous combination, the male (always AA) never shows the factors of the particular latent female type which it carries. These appear only when AA is reduced to Aa, that is, in the female organism.

GOLDSCHMIDT'S representation of the females was therefore

Achates	*Agenor*	*Laomedon*
$Aa\begin{cases} G^2G^2 \\ G^2G^1 \\ G^2G \end{cases}$	G^1G^1 G^1G	$G\,G$

The males correspond except for the additional factors AA. Simplified slightly this amounts to:

Achates	*Agenor*	*Laomedon*
$G'G'$	$G\,G$	$g\,g$
$G'G$	$G\,g$	
$G'g$		

GOLDSCHMIDT'S scheme, while accounting for the possible occurrence of all three types of female in one brood, failed, as pointed out by FREYER (1914), to explain the occurrence in *P. polytes* of three types in the brood

when the complete recessive (*laomedon* of *P. memnon*) is crossed with any of the other types. FREYER obtained matings of this sort that gave in each case the three types of female. Accordingly, GOLDSCHMIDT'S hypothesis broke down at this point, and two pairs of factors are necessary to explain all the facts presented by FREYER'S results, as PUNNETT (1910) had assumed on theoretic grounds (though assuming the male-like type to be dominant rather than recessive, as it later proved to be), as well as BAUR (1914), whose scheme applicable to both forms is as follows, *A* and *B* here referring to the interacting factors of female coloration.

Achates	*Agenor*	*Laomedon*
or	or	or
Romulus	*Polytes*	*Cyrus*
AABB	*AAbb*	*aaBB*
AABb	*Aabb*	*aaBb*
AaBB		*aabb*
AaBb		

Under the same scheme Colias would be:

White	*Yellow*
AA	*aa*
Aa	

It is understood that in the male other factors, determining its own coloration, are epistatic to these and render them latent.

It is this scheme which FREYER (1914) and PUNNETT (1915) employ. It fits fairly well all of FREYER'S data as well as those of JACOBSON (DE MEIJERE 1910). FREYER supplements the hypothesis by assuming that the male is always heterozygous for an inhibitor *Pp* (*Ii*, PUNNETT 1915) which prevents the appearance of the female coloration, i.e., the expression of the factors that determine it, while the female, *pp* (or *ii*) is always recessive for this factor.

The simpler explanation advanced by BAUR, PUNNETT and FREYER has since been adopted by GOLDSCHMIDT (1920).

SEX-CONTROLLED CHARACTERS IN *Argynnis paphia* AND *Bruchus quadrimaculatus*

GOLDSCHMIDT and FISCHER (1922) have recently described the heredity of a mutation in wing color in the female European silver-spot butterfly, *Argynnis paphia*. This somewhat "melanic" variation of the typically yellowish brown female is called *valesina*. Like the white variety in Colias, it depends upon a single dominant factor affecting the ground color of the wings.

Valesina occurs with the typical yellowish-brown female over the greater part of the palearctic realm. In the mountains of north China all females are *valesina*; eastward the proportion of black females to brown in the general population diminishes, and on the low plains of Central Europe *valesina* is rarely found with the type female, nor is it represented in North Africa and Japan. But in the Ukraine and in northeastern Germany it occurs in a somewhat high proportion; while in west Germany, some parts of France, and in the mountains of southern Switzerland, it is not rare.

With great skill and patience FISCHER bred in Zurich (1915-1919) four lines of stock from a single *valesina* female from northeast Germany (Königsberg).

Its mode of inheritance is very similar to that of the white variety in *Colias philodice* and *C. eurytheme*. The male is uniformly like the typical yellow-brown *paphia* female, but it may be genetically either *VV*, *Vv* or *vv* for female coloration.

Nine combinations of the three genotypes of the male with the three of the female are possible. Six are represented in FISCHER's cultures. They are as follows:

♀ *vv*×♂ *vv* gave 16 families, all *paphia* (except one waif).
♀ *vv*×♂ *Vv* gave 5 families: 104 *vv* (*paphia*)+68 *Vv* (*valesina*) females.
♀ *vv*×♂ *VV* gave 3 families: 168 *Vv*, all *valesina* (except one waif).
♀ *Vv*×♂ *vv* gave 11 families: 357 *vv*+353 *Vv* females.
♀ *Vv*×♂ *Vv* gave 13 families: 143 *vv*+367 (*VV*+*Vv*) females.
♀ *Vv*×♂ *VV* gave 1 family: 21 (*VV*+*Vv*) all *valesina* females.

Only once did a *Vv* (*valesina*) ♀ produce exclusively *valesina* daughters, having mated with a *VV* ♂. Homozygous *valesina* females did not appear as the mothers of distinct broods, though they were demonstrable as mothers of certain mixed broods, assuming that the wild fathers were *vv*. Hence *VV* is not lethal even in the female, but it may be semi-lethal or "relativ empfindlich," according to GOLDSCHMIDT, as the shortage of *valesina* shows (*Vv*×*Vv* gave an average of 2.57 *valesina*: 1 *paphia*, *versus* 3 : 1, and a shortage of *Vv* occurs in the cross ♀ *vv*×♂ *Vv*).

A study of GOLDSCHMIDT and FISCHER's (1922) *Vv*×*Vv* families shows that if we exclude three closely related fraternities: G, (23), (35), the remaining ten give a very close approximation to the 1 : 3 ratio, namely, 56 *vv* : 173 (*Vv*+*VV*), cf. 57.25 : 171.75, expectation. Of these three exceptional families, G, which is exactly midway between 1 : 3 and 1 : 2 (namely, 30 *vv* : 73 (*Vv*+*VV*)) produced a strain in which (23) = 30 *vv*+60 (*Vv*+(*VV*?)) and (35) = 27 *vv*+61(*Vv*+*VV*?) arose by *Vv*×*Vv* matings.

These clearly 1 : 2 ratios strongly indicate the action of a definite lethal factor linked with *V*, brought out by the inbreeding. The data from FISCHER'S Stammbaum (GOLDSCHMIDT and FISCHER 1922, pp. 269-273) showing how this took place are given in the diagram on page 540.

Family (23) = 30*vv* + 60*Vv* arose from a *Vv* × *Vv* mating between two parents belonging to family (10) all of which were *Vv*, which came from a *vv* ♀ of family G mated with a male that must have been *VV*. Therefore G does not show the full effect of the lethal factor, which may there appear "semi-lethal," hence the equivocal ratio.

Family (35) = 27*vv* + 61*Vv* similarly arose from a *Vv* × *Vv* mating from parents belonging to a wholly *Vv* family (19), produced by a *VV* ♂ (from family G) mated to a *vv* ♀.

This strain evidently carried a lethal factor closely linked with *V*. *VV* is so clearly strictly lethal and not semi-lethal in families (23) and (35), judging by the ratios, that one may doubt whether the shortage of *VV* individuals in G was due to the lethal factor.

GOLDSCHMIDT advances a physiological theory in explanation of sex-controlled heredity. Either (1) the chemical constituents necessary for the realization of certain genes are lacking in the male, though the genes are present, or (2), as seems to him more reasonable, at the moment of the development of wing pigment when a sex-controlled factor is about to play its part, differentiation in the male has already reached a point at which no further change is possible. Differentiation in the female, on the other hand, is not yet so far advanced, and the organism is therefore susceptible to the action of the genetic factor.

BREITENBECHER (1921) has recently discovered in the cow-pea weevil, *Bruchus quadrimaculatus*, sex-limited variations in the female. A series of multiple allelomorphs in body and elytral colors has been brought out by inbreeding: red, black, white and tan, stated in order of dominance, the ultimate recessive, tan, being the normal type. The males while all alike as regards their non-spotted, tan-colored elytra, resemble their respective females more or less in body color. Thus, the elytral coloration of the female is strictly sex-limited; body color in the female is only partially sex-controlled.

When these four varieties were first bred, the four elytral spots of the female were invariably black, whatever the ground color, but recently BREITENBECHER (1923) discovered a red-spotted female in pure red stock. Red-spotting was found to behave as a simple dominant to black-spotting. He has been able to combine red-spotting with each of the allelomorphic series of colors affecting body and elytra.

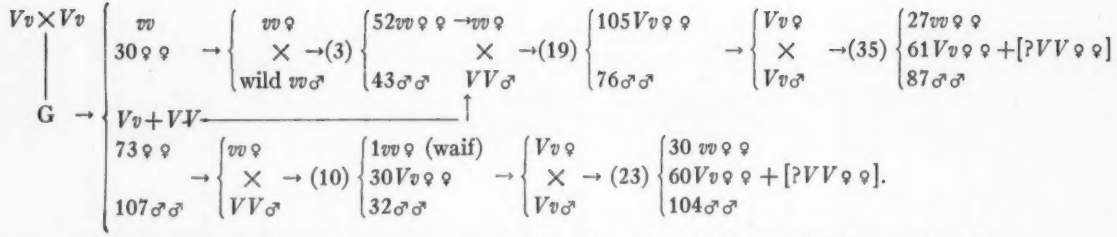


Diagram giving data from FISCHER's pedigree of *Argynnis paphia* and its yellowish-brown female mutant form *valesina*.

No unusual ratios are reported in these results, which are remarkably regular.

An interesting series of somatic variations in female coloration,—unilateral changes in elytral color, whereby one elytron takes on a color epistatic to that of its race-color and normal elytron,—has also been reported by BREITENBECHER (1922). Thus 22 black females were found that had one red elytron, 7 tan females with one black, one tan female with a single white elytron; and one white female with an elytron of black. These local somatic changes are ascribed to local nuclear or chromosomal mutations, similar to the corresponding mutations in germ cells, but they are not inherited.

SOME FACTS AND PROBLEMS OF SEX PHYSIOLOGY. COMPARATIVE VELOCITY OF DEVELOPMENT

The precocity of the male, as compared with the female, has often been observed in Lepidoptera and is well-marked in Colias. Attention was called to it in my preliminary paper. Males regularly appear in the field earlier than females, and in each laboratory culture the majority of the first half of each brood to emerge from the chrysalis, as a rule, are males. The male feeds for a shorter period, completing its larval development earlier, as a rule, than the females.

In *Papilio rutulus*, however, according to MUNSON (1906), females appear before the males, but testes develop earlier than ovaries. The sex cells of the testis of the male caterpillar were "in the spermatid stage" when the oldest egg in the ovary of the female caterpillar was in the "first stages of growth," mature spermatozoa being developed as early as the middle of the pupa stage.

DEMOLL (1908), on the authority of TEICH, states that in Argynnis males appear 8 to 14 days before females; in Pararge, 14 days. In the genera Apatura, Euripus and Hastina the males are flying, according to SEITZ (1894), weeks before the first females appear.

It is well known that in certain moths the female moults once more than the male. This is true of the genus Notolophus (Orgyia), as shown by the following table compiled from TUTT (1900):

	Number of moults		*Authority*
	Male	Female	
N. leucostigma	3	4	RILEY
N. gulosa	3–4	4	DYAR
N. antiqua (U. S.)	5	6	DYAR
N. antiqua (England)	3–4	4–5	CHAPMAN

CHAPMAN (1887) says in regard to *N. antiqua*, *à propos* of the fact that the male emerges from the pupa a few days before the female,

"If we consider only the 4-moulters, consisting of both males and females, this is not so, but if we associate them in this order—(1) 3-moulter males, 4-moulter females, (2) 4-moulter males, 5-moulter females, we find that the usual rule of the males emerging first is observed."

He adds that

"the male, though feeding as larva a shorter time (being a smaller insect), remains a longer time in the pupal state than the female, apparently requiring a longer time to undergo its full development."

The last statement is true of the honey-bee, in which the drones appear from one to four weeks before the females. BENTON (1899) gives the time required for development as follows:

	Egg	*Larva*	*Pupa*	*Total*
Queen	3	5½	7	15½ days
Worker	3	5	13	21 days
Drone	3	6	15	24 days

It thus appears that, although the sexes in insects differ in their velocity of development, the early appearance of the males does not necessarily imply a more rapid, and may even be associated with a slower, development. In the case of Notolophus, it involves one less moult.

A very remarkable case of this sex difference in the apparent velocity of development occurred in HARRISON'S (1920) hybrid cross between two geometrid moths, *Oporabia autumnata* ♀ (38 chromosomes) × *O. dilutata* ♂ (30 chromosomes), in which the F_1 *females* (*with no ovaries*) emerged *three months* before the males.

These females were more like *dilutata* in appearance, patroclinous, the males intermediate. HARRISON draws the obvious conclusion that the time of emergence of the mature insect depends upon the time of completion of gametogenesis.

In *Drosophila melanogaster*, it is well known that the female is slightly precocious, and in consequence has a slight advantage in the sex ratio, exactly the converse of the case of Colias. But in *Drosophila funebris*, STURTEVANT (1918) states, the reverse is true. This species resembles in this respect *Colias philodice* and *C. eurytheme*. "Males usually emerge in a little less time than the females" and "an excess of males is more frequent than excess of females." The disparity in the sex ratio in Drosophila, however, is much less than in Colias, due doubtless to the fact that Drosophila suffers much less from infectious diseases such as those which greatly affect the sex ratio in Colias by eliminating more of the slowly maturing females than males.

Hybridization of different species of Oporabia, as we have seen, not only changes profoundly the sex ratio but results in the precocious development of the female, owing to the non-development of the ovaries. In Colias, I have observed a similar though less well-marked tendency in hybrid crosses between *C. philodice* and *C. eurytheme*.

The sex ratio in a large healthy brood of either *C. eurytheme* or *C. philodice* approaches equality, with a slight excess of males. Thus families of *C. eurytheme* in early summer, in which the death rate from disease was comparatively small, were as follows:

	Males	*Females*
In 1913, a	57	53 and one gynandromorph
b	49	47
c	214	206
In 1914, x	149	136
y	29	28
In 1916, I	102	115
Total	600	585, a sex ratio of 1.025

In *C. philodice* families likewise raised from wild females in early summer (1909, 1910) gave a sex ratio of 1.4. Five broods produced by inbreeding in 1919 and 4 in 1920 gave a sex ratio of 1.026. Males were in excess in 6 of these 9 broods.

Males in both species are normally precocious, that is, the male members of any family emerge from the chrysalis earlier than their sisters. Similarly, the males appear in the field earlier than the females of their own generation. I have found that these well-known facts are due not to an earlier laying of male-producing eggs, but probably to a greater rapidity in the development of the male as compared with the female.

Hybridization of *C. eurytheme* with *C. philodice* sometimes upsets both the normal sex ratio and the usual precocity of the males. In other words, the females tend to appear earlier than the males and in greater numbers. This has occurred only in the cross *C. eurytheme* ♀ × *C. philodice* ♂, and, even in that case, not regularly. Yet it has been observed often enough in this cross, and is such a rare exception to the general rule, that it merits especial notice. The F_1 hybrids of *C. eurytheme* ♀ × *C. philodice* ♂ raised in the fall of 1912 were almost exclusively females.

Family	*Females*	*Males*
1912, a	11	1 (the last to emerge)
b	4	1
c	3	0
e	1	0
Total	19 ♀♀	2 ♂♂

In families of similar origin in 1913 (o and p) no marked precocity or abnormality in the sex ratio occurred, although in 1913, o, seven of the first nine to emerge were females. Nine of the first eighteen, however, were males. A similar family, 1913, v, showed a normal precocity of males. But in 1914 the same tendency to produce an excess of females, with the early appearance of individuals of that sex, recurred, being shown to remarkable degree in the only example of this particular cross (*C. eurytheme* ♀ × *C. philodice* ♂) raised that season, namely, d: 34 females, 20 males. Of the first 20 to emerge, 13 were females, only 7 were males. Families of the reciprocal cross raised at the same time gave the normal masculine precocity and excess in numbers.

It is possible that the partial sterility of the male F_1 hybrids may furnish a clue to the absence in their own generation of precocious males. The males of such families may be less viable than the females, and hence the embryos or larvae that should become the early-appearing males of the brood may perish before maturity, allowing a female detachment of the family to come first. The same idea may account for the fact that the identical phenomenon occurred in the back-crossing of the male F_1 hybrids with *C. eurytheme* in 1913. In such broods, r. s and t, females appeared first, although in a similar family, u, neither sex could be said to be precocious. In brood t, in which all the females were white, there was also an excess of females: 39 white females, 33 males.

The F_1 hybrids of the reciprocal cross, however, have not produced any families showing unusual sex ratios or precocities. Thus families, 1914, e, g, h and i, showed no precocity of either sex, though h (back-cross of such a female hybrid × *C. philodice*) gave an excess of females: 36, *versus* 25 males, and a group of five males emerged five days later than the rest of the brood, indicating retarded development.

Summary

The cross which involves the *philodice* male (but not the reciprocal cross), which in some cases produces sterile male offspring, produces, in some and indeed in most cases, an excess of females, whereas precocious males are conspicuously absent. Possibly the same cause that leads to sterility in the surviving male hybrids of such a family has led also to a lack of viability in their brothers that presumably have perished.

WHITMAN and RIDDLE (1919) found that hybridization of the Japanese turtle-dove (*Turtur orientalis*) with the white ring-dove (*Streptopelia alba*) produces in spring and summer "nearly all males," and if a female

of such a mating is made to "overwork at egg production," that is, not allowed to stop laying and incubate her eggs, she produces in late summer and autumn "all, or nearly all, female offspring."

This statement regarding the hybrid cross and the assertion that the first egg of each unlike pair ("clutch") laid in close succession, is usually a male, the second a female, has seemed to me to indicate a precocity of male-producing eggs comparable to the normal condition in Colias. Further examination of WHITMAN and RIDDLE'S published data, however, have shown that the extensive conclusions regarding sex control which RIDDLE has drawn appear to rest upon a rather small basis of published facts, as the following analysis may show.

In the cross *T. orientalis* ♀ × *alba* ♂ an excess of males is said to occur in the spring months, whereas later in the season, e.g., after July 1, females predominate. The offspring of three mothers are cited to establish this point.

♀ 99 had	4 ♂, 1 ♀	offspring before July 1;
	3 ♂, 6 ♀	offspring after July 1.
♀ 500 had	15 ♂, 6 ♀	offspring before July 1;
	25 ♂, 14 ♀	offspring after July 1.
♀ 54 had	10 ♂, 3 ♀	offspring before July 1;
	3 ♂, 13 ♀	offspring after July 1.
Total	29 ♂, 10 ♀	offspring before July 1;
	31 ♂, 33 ♀	offspring after July 1.

It is apparently on such meager data as these that RIDDLE'S sweeping conclusions regarding sex control are drawn. The numbers are small and indicate a slight excess of male offspring. The progeny of only one of the three mothers, namely, No. 54, seem to me to lend any support to RIDDLE'S conclusion, and the small numbers of offspring of this mother (13♂♂, 16♀♀) indicate that the seasonal variation in sex ratio is quite within the range of merely chance variations.

Yet, despite the small numbers, it seems evident that species hybridization involving the ♀ *T. orientalis* does produce noticeable fluctuations in the sex ratio, possibly in the long run an excess of males, but that the males appear earlier in the season than the females is not well supported by the examples that he cites.

WHITMAN and RIDDLE also found that in pure species, in which sex ratios are not upset by hybridization, the first egg of each two laid in close succession is usually a male, the second a female.

CUENOT (1900), working with homing pigeons, found, on the contrary, that in 30 cases observed, the male egg was laid first, in fifteen cases the

female egg, so that the idea of the precocity of the male egg, which had been noticed by breeders ever since the days of ARISTOTLE, was not supported by his observations. COLE (1915) working chiefly with Tumblers of diverse origin and a few Homers, likewise found no correlation between maleness and the first egg of the pair. RIDDLE (1916), however, regards these discordant results as due to the mongrel nature of the stock, which he assumes to have been used by these observers, and maintains that in the pure strains which Doctor WHITMAN bred the male-first rule holds.

As evidence, he uses the breeding records of two females of *Streptopelia risoria*, the pale ring-dove. The first of these females laid in 1913 nine pairs of eggs, each pair comprising one male and one female. In six of these pairs the male egg was laid first, in 3 the female egg. In the other case there were 12 such pairs; in 9 of which the male egg was laid first, in 3 the female egg. Such evidence is not very convincing.

The number of examples cited in support of the idea that in pure wild species the first egg of a pair (of different sexes) laid in succession is male is small. In *Stigmatopelia senegalensis* (Senegal turtle-dove) two pairs are cited in which the rule applies, in *Streptopelia risoria* (blond ring-dove) six, two showing the reverse; in *Phaps chalchoptera* (bronze-wing) four cases; in *Spilopelia suratensis* (Surate turtle-dove) four cases, while three show the reverse.

Data regarding pairs the sex of only one member of which is known are more extensive, but since the unknown member of the pair in half the cases, by the law of chance, should be of the same sex, the whole number of pairs to be included as evidence is twice that which it should be. In *S. senegalensis*, 19 pairs with one member unidentified are recorded (in all, 9 females, 10 males), 15 of which seem to follow the rule, 3 to contradict it; one is equivocal [no second (?) egg]. Two pairs of eggs of opposite sexes, as already stated, also follow the rule (*S. senegalensis*), which seems to be applicable to this species though not to *Spilopelia suratensis*.

In the hybrid cross, *S. alba* ♀ × *T. orientalis* ♂, 12 cases are cited of both sexes occurring in one clutch. The first-laid egg was male in 10, female in 2. This cross, as before noted, produces a predominance of males. In the reciprocal cross, the male egg was laid first in 7 cases out of 12; in 5 cases, the female egg came first. The probability that the *alba* mother was of hybrid origin is suggested by RIDDLE in explanation of the departure, in the last example, from the supposed rule.

In general the conclusion that the males appear earlier in the season or that the first egg of a clutch of two is usually male is not, in the writer's

opinion, proved by the published data, either for the cross involving the *alba* male or for any of the others.

SUMMARY AND CONCLUSIONS

1. In *Colias philodice* and in *C. eurytheme* there are two types of female, one with yellow wings like the male (though slightly paler) and one, less common, that is white. The common yellow, or male-like, type is recessive to the rarer white variety, the two being differentiated by a single pair of factors, W = white, w = yellow.

2. The male-like type of female in other butterflies has likewise proved to be recessive to the other female variety or varieties, i.e., *Argynnis paphia* ♀, to the dominant "melanic" variety *valesina* (GOLDSCHMIDT and FISCHER); *Papilio cyrus*, to *polytes* and *romulus* (FREYER); *P. memnon* var. *laomedon* (somewhat male-like), to *agenor* and *achates* (DE MEIJERE and JACOBSON); but in the species with trimorphic females certain individuals of the recessive, or male-like, type are dominant for a second pair of factors, for which the second, or intermediate, type of female is recessive; the third type of female is a homozygous or heterozygous double dominant.

3. Males in Colias are constantly yellow, even in broods (families) in which all the females are white.

4. Therefore white is not, by reversal of dominance, recessive in the male and lethal in homozygous combination, as assumed in my preliminary paper, and the exceedingly rare white "aberration" in the male, known to entomologists but as yet never bred in captivity, must be due to an entirely independent mutation, as predicted by GOLDSCHMIDT.

5. Males in any family correspond in genetic constitution to their sisters, being either

(a) *ww* (homozygous for yellow female coloration);
(b) *Ww* (heterozygous for white female coloration); or
(c) *WW* (homozygous for white female coloration).

6. Recessive yellow females (*ww*), mating with
   (a) males homozygous (*ww*) for recessive yellow female coloration, produce only yellow (*ww*) female offspring;
   (b) males heterozygous (*Ww*) for female coloration, produce equal numbers of heterozygous white and recessive yellow daughters;
   (c) males homozygous dominant (*WW*) for female coloration, should give only white heterozygous daughters. No brood from this type of mating has yet been raised.

7. Heterozygous white females (*Ww*), mating with
   (a) males homozygous (*ww*), produce equal numbers of heterozygous white (*Ww*) and recessive yellow (*ww*) daughters (this type of mating is the one that I have most commonly obtained);
   (b) males heterozygous (*Ww*), produce white and yellow daughters in the proportion 3 : 1, a result rarely realized in this stock, however, presumably because of the action of certain lethal factors;
   (c) males homozygous (*WW*), produce white daughters only
8. Homozygous white females (*WW*) mating with
   (a) heterozygous (*Ww*), males have produced white daughters only, but there is no certainty that in my cultures they have been mated with
   (b) homozygous *WW* males, and the combination with
   (c) homozygous *ww* males has not been accomplished.

9. Wild white females in the regions from which my stocks of *C. phil-odice* and *C. eurytheme* have come have invariably been heterozygous for white female coloration. Assuming that 5 percent of the females in any locality are white, 95 percent yellow, the proportion of homozygous to heterozygous white females would be as 1 : 78. If white females comprise 10 percent of the female population, heterozygous white females would be 38 times as common as the homozygous. Formulae and numerical tables computed by Professor J. W. YOUNG are given for estimating the proportions of homozygous and heterozygous whites in a population comprised of 5 to 50 percent of white females, 95 to 50 percent of yellow females, and equal numbers of males corresponding, respectively, genetically to the females.

10. Such a population is stable in its proportions after the first mating, but, if the homozygous dominant *WW* combination were constantly lethal, the white character, whether *Ww* or *WW*, would gradually disappear from the population and become extinct.

11. Great difficulty was experienced in demonstrating that the breeding of two heterozygotes for female coloration gives the 3 : 1 ratio. This was probably due to lethal factors brought out by the inbreeding. Finally, in 1920, stock apparently free from lethal factors produced a family showing a clear-cut 3 : 1 ratio. From it two successive generations of all-white-female families were raised.

12. Crossing this all-white-female stock the following spring with wild males free from the white factor showed that these white females were at least in part heterozygotes (presumably 50 percent homozygous, 50 percent heterozygous), for all that were tested proved to be heterozygous.

13. Unexpected ratios occur. All-white families are sometimes produced by two heterozygous parents. Moreover, 67 white : 36 yellow female offspring (i. e., 2 : 1) were in one case produced by a heterozygous white female, *Ww*, mated to a homozygous recessive for female coloration, *ww*. These facts may be explained by the assumption of a recessive lethal factor, closely linked with yellow, carried in heterozygous condition in certain strains. A lethal gene similar to that occurring in *C. philodice* was evident also in *C. eurytheme* and in hybrids between the two species.

14. Unpublished data from Mr. THOMAS E. BEAN show, so far as they go, that, in the wonderfully variable species, *Colias christina*, white female coloration is inherited substantially as in *C. eurytheme* and *C. philodice*, though in one instance intergrades between white and yellow in the same family are described, unlike anything seen in *C. philodice* and *C. eurytheme*, and explicable by the coöperation of modifying factors.

15. PIESZCZEK'S data on *Colias myrmidone* show that in the mountains of upper Styria, where var. *alba* ♀ is more common than the red or orange type, all-white families have been raised, as well as others indicating a heterozygous mother. At lower altitudes, near Graz, where *alba* comprises about 22 percent of the female population, white females are usually heterozygous, and red mothers, presumably after mating with heterozygous males, produce some white daughters.

16. It is an open question what rôle climate plays in different regions in determining the proportion between white and yellow females in the population of *C. myrmidone*, whether indirect, through natural selection, or direct, upon germ cells or developing embryos.

In *C. philodice* and *C. eurytheme* climate apparently has no such determining effect. Cold inhibits and heat stimulates the development of yellow and orange wing-scale pigments, but these effects are slight and fluctuating as compared with the sharply differentiating action of the genetic factors.

17. Precocity in the development of the male, which is so well marked in Colias and which was shown in my earlier paper not to be due to earlier laying of male-producing eggs, is correlated with earlier development of the germ cells. But the question of comparative velocity of development in male and female insects is complicated by the fact that the female in certain moths undergoes an additional moult, and that drone bees, though they appear 1 to 4 weeks before the females, develop more slowly than either queens or workers.

18. Hybridization between *C. eurytheme* ♀ and *C. philodice* ♂ sometimes upsets both the normal sex ratio (thus producing an excess of females)

and the usual male precocity. Possibly males in such families are less viable.

LITERATURE CITED

BAUR, E., 1914 Einführung in die experimentelle Vererbungslehre. 1. Aufl. 401 pp. *10 pls.* Berlin: Gebrüder Borntraeger.

BENTON, F., 1899 The honey bee; a manual of instruction in apiculture. Bull. U. S. Dept. Agric., Div. Entomol., No. 1 (n. s.), pp. 1-118, *pls. 1-11.*

BREITENBECHER, J. K., 1921 The genetic evidence of a multiple (triple) allelomorph system in Bruchus and its relation to sex-limited inheritance. Genetics **6:** 65-90.

1922 Somatic mutations and elytral mosaics of Bruchus. Biol. Bull. **43:** 10-22.

1923 A red-spotted sex-limited mutation in Bruchus. Amer. Nat. **57:** 59-65.

CHAPMAN, T. A., 1887 On the moulting of the larva of *Orgyia antiqua.* Entomol. Monthly Mag. **23:** 224. Quoted from TUTT (1900).

COLE, L. J., and KIRKPATRICK, W. F., 1915 Sex ratios in pigeons, together with observations on the laying, incubation, and hatching of the eggs. Agric. Exper. Sta., Rhode Island State Coll., Bull. 162, pp. 463-512.

CUÉNOT, L., 1900 La distribution des sexes dans les pontes des pigeons. Compt. Rend. Soc. Biol., Paris, **52:** 870-872.

DEMOLL, R, 1908 Die Bedeutung der Proterandrie bei Insecten. Zoöl. Jahrb., Abt. Syst. **26:** 621 628

EDWARDS, W. H., 1868-1897 The butterflies of North America. Series I. Philadelphia: Amer. Entomol. Soc. 1868-1872. Series II. Boston: Houghton, Mifflin and Co. 1884. Series III. Boston and New York: Houghton, Mifflin and Co. 1897.

FREYER, J. C. F., 1914 An investigation by pedigree breeding into the polymorphism of *Papilio polytes* Linn. Phil. Trans. Roy. Soc. London, B **204:** 227-254.

GEROULD, J. H., 1911 The inheritance of polymorphism and sex in *Colias philodice.* Amer. Nat. **45:** 257-283.

1921 Blue-green caterpillars: the origin and ecology of a mutation in hemolymph color in *Colias* (*Eurymus*) *philodice.* Jour. Exp. Zoöl. **34:** 385-412. *pl. 1.*

GOLDSCHMIDT, R., 1912 a Erblichkeitsstudien an Schmetterlingen I. Zeitschr. f. indukt. Abstamm. u. Vererb. **7:** 1-62. *2 pls.*

1912 b Bemerkungen zur Vererbung des Geschlechtspolymorphismus. Zeitschr. f. indukt. Abstamm. u. Vererb. **8:** 79-88.

1916 Experimental intersexuality and the sex problem. Amer. Nat. **50:** 705-718.

1917 A further contribution to the theory of sex. Jour. Exp. Zoöl. **22:** 593-611. *pls. 1-3.*

1920 a Untersuchungen über Intersexualität. Zeitschr. f. indukt. Abstamm. u. Vererb. **23:** 1-212. *11 plates.*

1920 b Mechanismus und Physiologie der Geschlechtsbestimmung. 251 pp. Berlin: Gebrüder Borntraeger.

1921 Geschlechtsbestimmung. Festschr. d. K. Wilhelm Gesellsch. z. Förderung d. Wissenschaften, zu ihrem 10-jährigen Jubiläum. pp. 90-95. Berlin.

GOLDSCHMIDT, R., and FISCHER, E., 1922 *Argynnis paphia-valesina,* ein Fall geschlechtskontrollierter Vererbung bei Schmetterlingen. Genetica **4:** 247-278.

HARRISON, J. W. H., 1920 Genetical studies in the moths of the geometrid genus Oporabia (Oporinia) with a special consideration of melanism in the Lepidoptera. Jour. Genetics **9:** 195-280.

HOPKINS, F. G., 1894 The pigments of the Pieridae. A contribution to the study of excretory substances which function in ornament. Proc. Roy. Soc. London **57:** 5-6.

1896 On the pigments of the Pieridae: a contribution to the study of substances that function in ornament. Phil. Trans. Roy. Soc. London B **186:** 661-682.

JACOBSON, E., 1909 Beobachtungen über den Polymorphismus von *Papilio memnon* L.♀. Tijdschr. v. Entomol. **52**: 125-157.

JENNINGS, H. S., 1916 The numerical results of diverse systems of breeding. Genetics **1**: 53-89.

MEIJERE, J. C. H. de, 1910 Über Jacobsons Züchtungsversuche bezüglich des Polymorphismus von *Papilio memnon* L.♀, und über die Vererbung secundärer Geschlechtsmerkmale. Zeitschr. f. indukt. Abstamm. u. Vererb. **3**: 161-181.

MORGAN, T. H., 1914 Sex-limited and sex-linked inheritance. Amer. Nat. **48**: 577-583.

MUNSON, J. V., 1906 Spermatogenesis of the butterfly, *Papilio rutulus*. Proc. Boston Soc. Nat. Hist. **33**: 43-124. *pls. 12-17.*

PIESZCZEK, A., 1917 *Colias myrmidone* Esp. Die Stammform und ihre Abarten in Oesterreich-Ungarn. 69 pp., *3 colored pls.* Wien: Oesterreichischer Entomol. Ver.

POLL, H., 1909 Zur Lehre von den sekundären Geschlechtscharakteren. Sitzber. d. Gesell. Naturforsch. Freunde zu Berlin. No. 6: 331-352, *2 pls.*

PRELL, H., 1915 Über die Beziehungen zwischen primären und sekundären Sexualcharakteren bei Schmetterlingen. Zoöl. Jahrb. Allgem. **35**: 183-224, 593-602, *Taf. 6-9.*

PUNNETT, R. C., 1910 "Mimicry" in Ceylon butterflies, with a suggestion as to the nature of. polymorphism. Spolia Zeylandica **7**: 1-24, *pls. 1-2.*

1915 Mimicry in butterflies. 188 pp., *16 colored plates.* London: Cambridge University Press.

RIDDLE, O., 1914 The determination of sex and its experimental control. Bull. Amer. Acad. Med. **15**: 1-20.

1916 Sex control and known correlations in pigeons. Amer. Nat. **50**: 385-410.

1917 Control of the sex ratio. Jour. Washington Acad. Sci. **7**: 319-356.

SCUDDER, S. H., 1889 The butterflies of the eastern United States and Canada. 3 vols., 1956 pp., *89 pls., 3 maps.* Cambridge, Massachusetts: Published by the author.

SEITZ, A., 1894 Allgemeine Biologie der Schmetterlinge. III. Fortpflanzung. Zoöl. Jahrb. Abt. Syst. **7**: 823-851.

STANDFUSS, M., 1896 Handbuch der paläarktischen Gross-Schmetterlingen für Forscher und Sammler. 392 pp., *8 pls.* Jena: G. Fischer.

1913 Einige Andeutungen bezüglich der Bedeutung, sowie über Verlauf und Ursachen der Herausstaltung der sexuellen Färbungs-Dimorphismus bei den Lepidopteren. Mitth. d. Schweizerischen entomol. Gesellsch. **12**: 99-113.

STECHE, O., 1912 Die 'secundärer' Geschlechtscharaktere der Insekten und das Problem des Geschlechts. Zeitschr. f. indukt. Abstamm. u. Vererb. **8**: 284-291.

STURTEVANT, A. H., 1918 A parallel mutation in *Drosophila funebris*. Science N. S. **48**: 72-73.

TUTT, J. W., 1900 Natural history of the British Lepidoptera. **2**: 12. London: Swan, Sonnenschein and Co.

WENTWORTH, E. N., 1912 Another sex-limited character. Science N. S. **35**: 986.

1916 A sex-limited color in Ayrshire cattle. Jour. Agric. Res. **6**: 141-147.

WHITMAN, C. O., 1919 Posthumous works; edited by OSCAR RIDDLE. Inheritance, fertility, and the dominance of sex and color in hybrids of wild species of pigeons. Carnegie Inst. of Washington. Publ. 257, Vol. 2, pp. x+224, *39 pls.*

WOOD, T. B., 1905 Note on the inheritance of horns and free colors in sheep. Jour. A c. Sci. **5**: 364-365. *pl. 4.*

THE ASSOCIATION OF SIZE DIFFERENCES WITH SEED-COAT PATTERN AND PIGMENTATION IN *PHASEOLUS VULGARIS*[1]

KARL SAX

Maine Agricultural Experiment Station, Orono, Maine

Received May 26, 1923

TABLE OF CONTENTS

	PAGE
INTRODUCTION	552
Genetic behavior of crosses	553
Seed weight of various classes of segregates	554
The nature of size factors in beans	557
SUMMARY	559
LITERATURE CITED	560

INTRODUCTION

The work of EAST, EMERSON, HAYES and others with plants, and CASTLE'S work with animals, show that inherent size differences are apparently dependent on Mendelizing factors. In some cases, such as habit of growth in peas and beans and certain abnormal characters in maize, the quantitative characters involved are dependent on single factor differences, although in most cases many factors are involved and simple ratios are not obtained. In fact there is some evidence to show that quantitative differences may sometimes depend on genetic factors in most or all of the chromosomes.[2]

The multiple-factor hypothesis of size inheritance does not necessarily mean that the various factors are equal in effect or that they are interdependent for their expression. The relative effect of various factors and the cumulative effect of factor combinations have been difficult to analyze because the size factors could not readily be isolated and studied independently. If, however, certain size factors can be found linked with factors for qualitative characters it should be possible to study independently the size factor or factors within each linkage group. This is now possible in a limited way with the size differences in beans.

[1] Papers from the Biological Laboratory of the MAINE AGRICULTURAL EXPERIMENT STATION, No. 157.

[2] In a recent paper, GATES (1923) maintains that increased variability of petal size in the F_2 of Oenothera hybrids is not due entirely, at least, to Mendelian size factors, and suggests that "perhaps sizes in general, where repeated in the same organism, are not Mendelian in their inheritance."

The work of TSCHERMAK, EMERSON, SHULL and SPILLMAN on the inheritance of vine and seed-coat characters in the bean has been reviewed by SHAW and NORTON (1918) who find the earlier hypotheses in accord with the results of their own extensive studies. Pigmentation is dependent on a factor *P*. Total pigmentation is dependent on an extension factor *T*, the recessive of which results in a partially pigmented or "eyed" bean. Mottling is, according to the theory of SPILLMAN and EMERSON, dependent on two factors *Y* and *Z* in the same chromosomes. *Y* and *Z* may also exist separately in non-mottled beans and when brought together in crosses give mottled beans which seldom if ever become homozygous for mottling. Other factors control type of mottling and color of pigmentation. The inheritance of pattern and pigmentation in beans is often complex because of the numerous factors usually involved.

The parental varieties used in the present study include two varieties classed under the local names of Improved Yellow Eye and Dot Eye. In the Improved Yellow Eye the pigment is uniform or "solid" (self-colored) and is restricted to the area around the hilum and covers from a quarter to a third of the surface of the bean. The Dot Eye has only a very small pigmented area at either end of the hilum. In both of the eyed varieties the color of the pigment is yellow. For the non-pigmented parents several pure lines of small white beans were used. In all cases the pigmented varieties were about twice as large as the white varieties.

The parents and F_1 plants and all F_2 plants which were continued to F_3 were grown in an insect-proof cage to prevent uncontrolled cross-pollination, although cross-pollination does not occur frequently in the field. All F_2 beans for which weight records were made were grown in 1920. A glass scale designed by the writer (SAX 1921) was used for obtaining individual bean weights. The average seed weight in centigrams was obtained for F_2 and F_3 segregates. Most of the field work and description of F_2 segregates has been done by H. C. MCPHEE. The parental varieties were obtained from selections made by Doctor FRANK SURFACE.

GENETIC BEHAVIOR OF CROSSES

The genetic behavior of some of the crosses is shown in table 1. In the cross Improved Yellow Eye × White 1333 the F_1 was dark mottled and the F_2 gave a ratio of 27 mottled : 9 self-colored : 12 eyed : 16 white. The χ^2 test for goodness of fit gives a value of P = .83. The proportion of mottled and self segregates indicates that both of the mottling factors, *Y* and *Z*, were carried in the same chromosome by the white parent. The extension factor and factors for black, brown and purple color were also

carried by the white parent but could not be brought into expression until combined with the pigmentation factor *P*.

In the cross Dot Eye × White 1228 the F_1 was mottled. The approximately equal number of mottled and self-colored beans in F_2 indicates that the mottling factor *Y* came from one parent and factor *Z* from the other parent. The proportion of eyed beans is somewhat too large to result from two recessive factors and too small to result from a single factor, but otherwise the theoretical ratio fits very well (P = 0.57). It is assumed that two extension factors are present in 1228 because such a hypothesis is in accord with the results in the following cross.

TABLE 1

Segregation of pattern types in F_2 of eyed×white crosses.

CROSS	MOTTLED	SELF-COLORED	EYED	WHITE	TOTAL	GOODNESS OF FIT
Improved Yellow Eye 1310×White 1333	150	51	68	80	349	
Theoretical for 27 : 9 : 12 : 16 ratio	147	49	65	87		P = .83
Dot Eye 1902×White 1228	93	101	28	67	289	
Theoretical for 90 : 90 : 12 : 64 ratio	102	102	14	72		P = .001
Improved Yellow Eye 1317×White 1228	82	44	12	41	179	
Theoretical for 45 : 3 : 16 ratio	126		8	45		P = .32

The cross Improved Yellow Eye × White 1228 gave a purple mottled F_1 and a very complex segregation in F_2. The entire F_2 was carried to the F_3 and it was found that no mottled beans bred true. If *Y* came from one parent and *Z* from the other then no homozygous mottled beans should be obtained except by crossing over, but the ratio of mottled to self-colored should be 1 : 1. By grouping all completely pigmented beans a fairly good 45 : 3 : 16 ratio is obtained. Total pigmentation is apparently effected by two extension factors the double recessives of which result in eyed beans.

SEED WEIGHT OF VARIOUS CLASSES OF SEGREGATES

In all crosses the pigmented parent was at least twice as large as the non-pigmented parent. The large parents contributed large size of bean, the pigmentation factor *P*, the recessive or recessives of the extension factor which results in eyed beans, and one of the mottling factors. If size factors are present in most or all of the chromosomes, then there should be some correlation between pigmentation and pattern of F_2 beans and size. In all crosses of large pigmented varieties with small white varieties, involving 3865 progeny, the white segregates were signifi-

cantly smaller than the pigmented segregates. The relation between pigmentation and pattern and average bean weight of F_2 plants is shwno for several of the larger populations in table 2.

TABLE 2

Showing average seed weight in centigrams, of parents, and mean seed weight of various classes of segregates in F_2 and F_3 of certain bean crosses.

PARENTS				F_2 SEGREGATES				
♀	*Weight*	♂	*Weight*	*Mottled*	*Self*	*Eyed*	*White*	*Total*
I. Y. E. 1310	56. ± .5	White 1333	28 ± .9	39.1 ± .4	36.5 ± .5	39.0 ± .4	33.8 ± .4	349
Dot Eye 1902	58. ± 1.2	White 1228	21 ± .2	27.8 ± .4	27.7 ± .4	26.6 ± .5	23.4 ± .5	150
I. Y. E. 1317	48. ± .5	White 1228	21 ± .2	28.8 ± .4	28.6 ± .6	31.3 ± 1.1	26.4 ± .5	179
I. Y. E. 1317	48. ± .5	White 1228F_3	21 ± .2	29.2 ± .1	29.0 ± .1	30.2 ± .2	25.8 ± .1	2438

In the cross Improved Yellow Eye ($P\ t\ \widehat{yZ}$ or $P\ t\ \widehat{Yz}$) × White 1333 ($p\ T\ \widehat{YZ}$) all pigmented classes are significantly larger than the white F_2 segregates. The mottled and eyed F_2 segregates are also significantly larger than the uniformly pigmented or self-colored beans. It might be expected that large size would be associated with the eyed factor as large size and eyed came in from one parent, but the increased size of the mottled segregates is unexpected as the mottling factors were apparently contributed by the smaller parent. However, if the mottling hypothesis is correct then two-thirds of the mottled beans will carry the Improved Yellow Eye chromosome which carries one of the mottling factors and probably a factor for large size. It is also possible that the chromosome from the small white bean which carries the mottling factor carries a factor for large size. The small bean could carry several factors for large size and yet be relatively small due to the predominance of factors for small size. No significant correlation was found between bean weight and color of pigment in this cross.

There is no significant difference in size of the pigmented classes of F_2 segregates in the cross Dot Eye ($P\ t\ t\ \widehat{yZ}$) × White 1228 ($p\ T\ T\ \widehat{Yz}$). The mottled and solid segregates are somewhat larger than the eyed segregates but this difference is only twice the probable error and is of doubtful significance. All classes of pigmented segregates are significantly larger than the white segregates. The difference between the weight of eyed and white segregates is 4.6 times the probable error. The fact that there is no difference between size of mottled and self-colored segregates indicates that the chromosomes which carry the mottling factor in this cross carry different size factors than those in the preceding cross.

The weights of the different classes of segregates in both F_2 and F_3 are shown for the cross Improved Yellow Eye ($P\ t\ t\ \widehat{yZ}$) $\times$ White 1228 ($p\ T\ T\ \widehat{Yz}$). The pigmented classes are all heavier than the F_2 white segregates although the differences are only about 3 times the probable error in case of the self-colored and mottled segregates. The eyed segregates are larger than the other pigmented classes although the difference is of doubtful significance in F_2 because of the few individuals. In F_3, however, it is clear that the eyed segregates are significantly larger than the mottled or self classes. There is also some correlation between bean weight and eye pattern in F_3. The eye types were divided into 8 classes ranging from dot eye to almost completely pigmented. The correlation between eye type and bean weight for 307 eyed segregates gave a correlation ratio of $.30 \pm .04$. The dot-eyed and types similar to Improved Yellow Eye were smallest, while intermediate types were largest. It was also found that among the self-colored and mottled F_3 classes the yellow and brown segregates were heavier than the purples and reds. The difference is more than twelve times the probable error. The genetic behavior of the various colors is very complex and has not been completely worked out.

TSCHERMAK (1922) finds some evidence for segregation in size of beans borne on the F_1 plant. In the above cross the coefficient of variability for weight of beans on the F_1 plants was $18.0 \pm .7$ as compared with $10.8 \pm .9$ and $11.7 \pm .7$, respectively, for the parents. There is, however, little indication that the increased variability of F_1 is due to genetic factors for bean size. The correlation between bean weight of F_1 and bean weight in F_2 was found to be $.08 \pm .06$ (η). For F_1 bean weight and F_2 plant height $\eta = .36 \pm .05$, but this relation may be due to greater reserve food in the larger beans. There was no significant correlation between F_1 bean weight and F_2 pattern ($\eta = .10 \pm .06$).

Bean size is apparently not greatly influenced by plant height. In the above cross (Improved Yellow Eye $\times$ 1228) the correlation between F_2 bean weight and F_2 plant height gave a value of $r = .05 \pm .06$. For F_2 pattern and F_2 plant height $\eta = .12 \pm .06$. These correlations were determined because it was thought that since pigmented beans often have darker foliage than white beans that there might be an increase in plant size with darker foliage and perhaps some relation between plant size and bean weight. However, the large eyed beans used in this cross have white blossoms and pale green foliage,—a characteristic of all eyed and white beans used as parents.

Crosses of pigmented beans which differ in size also show association of size differences with pattern. In the cross of Improved Yellow Eye 1318 (weight = 52.1 ± .8) × Cranberry 1906 (weight = 70.0 ± 1.6) the F_2 mottled class had a mean weight of 56.9 ± .9; self-colored beans weighed 55.3 ± .7; while the eyed segregates weighed only 50.5 ± .8 centigrams.

THE NATURE OF FACTORS INVOLVED IN SIZE DIFFERENCES IN BEANS

So far as data are available, the behavior of the inheritance of size differences is in accord with the eight requirements proposed by EAST (1916) to test the multiple-factor hypothesis. No data on weight of F_1 beans were taken and even if F_1 weights were available they would be of little value due to paucity of numbers. The parents were pure lines and had been grown in a screened cage for six years so that the F_1 should be no more variable than the parents. The variability of the F_2 is greater than that of the parents. The grandparental types are occasionally recovered. There is a significant correlation between size of F_2 and resulting F_3 segregates. For Improved Yellow Eye × White 1228 this correlation gave a value of $r = .33 \pm .01$.

The number of size factors involved was estimated by CASTLE'S (1921) formula and by several other methods. These various methods give the number of size factors as about 4 to 6 in two of the crosses and more than 6 in the third cross (Dot Eye × 1228). However, the various assumptions necessary in estimating the number of size factors, based on F_2 distribution, make the results obtained of little or no value as SHULL (1922) has pointed out.

It is possible in these bean hybrids to determine the effect of a single factor or a group of closely linked factors. In this discussion an independent size factor may be taken to mean a single factor or several closely linked factors. In the cross Improved Yellow Eye × 1228 the pigmented beans had a mean weight of 29.0 while the white segregates weighed 26.4 centigrams. The pigmented F_2 segregates consist of homozygous and heterozygous individuals in the ratio of 1: 2. The genetic constitution of F_2 pigmented segregates was determined from F_3 behavior. The failure of a white segregate to appear in 8 or more F_3 segregates from a single F_2 pigmented plant was taken to indicate that the F_2 plant was homozygous for *P*. The chances are ten to one that an F_2 plant is homozygous for pigmentation if no whites appear in 8 F_3 progeny (see MULLER 1923). The F_2 segregates homozygous for pigmentation, and therefore homozygous for at least one size factor, except for crossing over, were significantly larger than heterozygous individuals. The average weight of

the 45 homozygous segregates was $30.7 \pm .6$, while the mean weight of 80 F_2 segregates heterozygous for size was $28.3 \pm .3$. The difference in weight of these classes is more than three times the probable error. The homozygous segregates (PP) were $4.3 \pm .8$ centigrams heavier than the white segregates (pp), while heterozygous F_2 individuals (Pp) were $1.9 \pm .6$ centigrams heavier than the non-pigmented class. Thus, both allelomorphs for large size which are associated with P control about 16 percent of the parental difference, while the factor in a heterozygous condition controls about half of this amount. In this case two factors have approximately double the effect of one factor within a single homologous pair of chromosomes, indicating that there is no dominance of size factors. The size factor or factors associated with the eye factors also cause an increased weight above that of the totally pigmented beans. The size factor or factors associated with the extension or eye factors have only about half the effect on seed weight as the size factor linked with the pigmentation factor, indicating that different size factors may not have an equivalent effect. This difference in effect of size factors may, however, be attributed to greater frequency of crossing over between the eye factor and size factors than between pigmentation factors and size factors.

In the cross Improved Yellow Eye $\times$ 1333 the pigmented F_2 segregates have a mean weight of $4.8 \pm .5$ centigrams heavier than the mean weight of the white segregates. It was not possible to compare the size factors in the heterozygous and homozygous condition since the F_3 was not grown to test the genetic constitution of F_2 segregates. Size factors are also associated with mottling and extension factors in this cross.

In the cross Dot Eye $\times$ White 1228 the pigmented segregates are $4.2 \pm .6$ centigrams heavier than the white segregates, so that about 11 percent of the parental difference is controlled by the factors associated with pigmentation, two-thirds of which are heterozygous.

In these crosses the factor or factors associated with pigmentation control about 4 or 5 centigrams of seed weight or about one-fifth or one-sixth of the difference in weight of the parental varieties. If the size factors in other linkage groups have a similar effect then the number of factors involved in the various crosses is about 5 or 6. However, the size factors in different linkage groups may not have the same effect on seed weight as shown by the comparison of the mean weight of totally pigmented, eyed, and white segregates in the cross Improved Yellow Eye $\times$ 1228.

The size factors in beans are independent in causing increased seed weight and several factors have a cumulative effect. Even within a

single homologous pair of chromosomes the allelomorphic factors in the homozygous condition have double the effect of a single factor in the heterozygous condition. These results are not in accord with behavior of size factors in rabbits. CASTLE (1922) finds that size factors are present in most or all of the chromosomes and yet there is no association of size difference with any one of four independent color and pattern factors. Accordingly, CASTLE concludes that the size factors in rabbits are interdependent for their expression.

The fact that a size factor in the $1n$ or heterozygous condition has only half the effect that it does in the $2n$ or homozygous condition is of interest in connection with JONES'S (1917) heterosis hypothesis. If all of the size factors in Phaseolus behave in a similar way then no hybrid vigor would be expected. As a matter of fact TSCHERMAK'S (1922) data indicate that in bean crosses the F_1 seed weight is less than that of the mid-parent. As shown in table 2 the mean weights of F_2 classes are less than the weight of the mid-parent. The decreased weight may be due to the dominance of some of the weight factors contributed by the smaller parent, or it may be attributed to heterozygosis. Since there is an inverse ratio between number of beans per plant and bean weight it is possible that heterozygosis increases fecundity and thereby decreases seed weight.

SUMMARY

Crosses between certain eyed (partially pigmented) and white beans resulted in completely pigmented mottled beans in F_1 and mottled, self-colored, eyed, and white beans in F_2. Mottling is dependent on two factors in the same linkage group, both of which are necessary to produce mottling. Completely pigmented beans are dependent on either one or two extension factors, the recessives of which result in eyed beans. Pigmentation is dependent on a single factor.

In all crosses of large pigmented beans with small white beans the pigmented F_2 segregates had a mean seed weight greater than that of the white segregates. In the cross Improved Yellow Eye $\times$ White 1228 the difference in average-seed weight between homozygous pigmented F_2 segregates and white segregates was found to be about one-sixth of the F_2 range. The difference between the weight of heterozygous pigmented F_2 segregates and white segregates is only about half as great as the difference between homozygous pigmented individuals and the white segregates. Thus, a size factor (or group of closely linked factors) in the $1n$ or heterozygous condition has only about one-half of the effect that it has in the $2n$ or homozygous condition. This lack of dominance is of

interest in connection with the hybrid-vigor hypothesis. Factor differences for seed weight are also associated or linked with one or both of the eye factors, with eye pattern factors, and with factors which determine the color of the pigment. Size differences even in case of blending inheritance where several factors are involved, may be effected by the independent action of the size factors in different linkage groups. These factors, when combined, have a cumulative effect. The size factors in different chromosomes may not be equal in their effect.

LITERATURE CITED

CASTLE, W. E., 1921 An improved method of estimating the number of genetic factors concerned in cases of blending inheritance. Science, N. S. **54**: 223.

1922 Genetic studies of rabbits and rats. Carnegie Inst. of Washington Publ. 320, pp. 3-55.

EAST, E. M., 1916 Studies on size inheritance in Nicotiana. Genetics **1**: 164-176.

GATES, R. R., 1923 A peculiar type of variability in plants. Jour. Genetics **13**: 13-45.

JONES, D. F., 1917 Dominance of linked factors as a means of accounting for heterosis. Genetics **2**: 466-479.

MULLER, H. J., 1923 A simple formula giving the number of individuals required for obtaining one of a given frequency. Amer. Nat. **57**: 66-73.

SAX, K., 1921 Simple device for weighing seeds. Bot. Gaz. **71**: 399.

SHAW, J. K., and NORTON, J. B., 1918 The inheritance of seed-coat color in garden beans. Massachusetts Agric. Exp. Sta. Bull. 185, pp. 58-104.

SHULL, G. H., 1921 Estimating the number of genetic factors concerned in blending inheritance. Amer. Nat. **55**: 556-564.

TSCHERMAK, E. VON, 1922 Über die Vererbung des Samengewichtes bei Bastardierung verschiedener Rassen von *Phaseolus vulgaris*. Zeitschr. f. indukt. Abstamm. u. Vererb. **28**: 23-52.

INHERITANCE OF WHITE SEEDLINGS IN MAIZE[1]

M. DEMEREC

Station for Experimental Evolution, Cold Spring Harbor, New York

Received May 28, 1923

TABLE OF CONTENTS

	PAGE
INTRODUCTION	562
Material and methods	563
Experimental results	564
Intercrosses	564
Genotype w_2 w_2	565
Cross between stocks 3 and 1	566
Cross between stocks 6 and 1	566
Crosses for linkage	567
Test of w_2-sh	568
Test of w_2-l_g	569
Test of w_2-v	569
Test of w_2-d	570
Test of w_2-p_r	570
Genotype w_4 w_4	570
Cross between stocks 2 and 4	570
Linkage relations	571
Test of w_4-w_a-s_u	572
Test of w_4-w_a-y	573
Test of w_4-w_a-y_p	574
Cross between stocks 6 and 2	574
Genotypes w_5 w_5 and w_6 w_6	575
Cross between stocks 11 and 3	575
Linkage between w_5 and y	575
Free segregation between w_7 and y	577
A 9 : 1 ratio	577
Linkage with endosperm color	578
A 28.6 : 1 ratio	580
A 9 : 7 or 2.08 : 1 ratio	580
Genetical constitution of F_1 plants	581
Summary of results of the cross 11 and 3	582
Genotype w_7 w_7	582
Cross between stocks 8 and 3	582
Genotypes w_8 w_8 and w_9 w_9	583
A 63 : 1 ratio	584
SUMMARY	584
LITERATURE CITED	585
APPENDIX—Tables 28 to 38	586

[1] Paper No. 109, Department of Plant Breeding, CORNELL UNIVERSITY, Ithaca, New York.

INTRODUCTION

White seedlings are characterized by the lack of chlorophyll. Under ordinary conditions, they die in the early seedling stage soon after the reserve food of the seed is exhausted. In color they vary from pure white to more or less creamy yellowish. Occasionally, individual plants have small amounts of yellowish-green tissue.

White seedlings are observed frequently in the higher plants. Most of those studied have been found to be simple recessives to the normal green. NILSSON-EHLE (1922) reported three independent factors for white seedlings which were found in different varieties of barley, and TROW (1916) showed that the white phenotype in *Senecio vulgaris* L. is determined by duplicate genes.

HALSTED and KELSEY (1904) described white seedlings in maize. Later, EMERSON (1912) and GERNERT (1912) presented evidence that the albinism studied is determined by a factor which is a simple Mendelian recessive to green. MILES (1915) furnished additional data on the inheritance of white seedlings, and made a cytological study of the albinos. He concluded that plastids are entirely absent in white plants. LINDSTROM (1918, 1920, 1921) studied the relations between white seedlings and some other chlorophyll types. RANDOLPH (1922) studied white seedlings cytologically and found plastid primordia present in all cells which normally would be green. In the extreme tip of the leaf he observed a limited region in which the cells contained green chloroplasts. He concluded that in the case of white seedlings "failure of the plant to become green is not to be explained as the result of an absence of plastids or plastid primordia."

White seedlings occur very frequently in corn; they can be observed in practically every corn field. Interesting data were obtained by HUTCHISON (1922)[2] on the presence of white seedlings in commercial varieties of corn. From 419 lots of seed collected from the northern experiment stations and seed companies, 1814 selfed ears were tested in the greenhouse; 144 of them, representing 22.4 percent of the lots, were found to throw white seedlings. The percentage might have been still higher if more ears had been selfed in certain lots. In 24 percent of the lots one ear only was selfed and in 16 percent of all the lots two ears; this lowered the chance of detecting white seedlings.

[2] With permission of Director C. B. HUTCHISON, original data are used and arranged in such a way that the frequency of occurrence of white seedlings can be shown.

MATERIAL AND METHODS

This study was taken up as the result of a need felt by workers on maize for more endosperm and seedling characters for use in linkage tests. A systematic search for seedling characters was begun during the winter of 1919–1920, a sample of seed being planted for this purpose from each available self-pollinated ear. To facilitate this search Professor R. A. EMERSON and Dr. E. G. ANDERSON made available to the writer all the selfed ears accumulated in the course of their studies on maize.[3] Many distinct variations were found, the majority affecting the development of chlorophyll. Among the ears tested, 15 were segregating for white seedlings. Twelve of them came from unrelated families. Progenies in these ears gave the material for the beginning of this investigation.

Some additional material was obtained in the spring of 1921 and 1922 from Professor C. B. HUTCHISON.

An effort was made to determine the relation of these white seedling characters to each other by intercrossing. This is rendered rather difficult by the lethal nature of the white seedling character. Heterozygous green plants must be used in crossing. These are not visibly different from their homozygous green sibs. In any selfed family throwing white seedlings, two-thirds of the green plants are expected to be heterozygous, and of random intercrosses between plants of such families, four-ninths are expected to be crosses between two heterozygous plants. But in order to be dependable both parents of the cross must be selfed. This was often impossible because most of the plants produced only one ear. Where the lines to be crossed differed by some aleurone or endosperm character, this difficulty was more easily overcome. The dominant parent was selfed while the recessive parent was pollinated by a mixture of its own pollen with pollen from the dominant parent. The crossed seeds were indicated by xenia.

In the cases where the white seedling character is dependent upon more than one Mendelian factor the chances for successful crosses are lower.

Linkage tests with other factors have been made, but these are as yet far from complete. In a few cases they have proved valuable in identifying the factors involved.

[3] The writer is greatly indebted to Professor R. A. EMERSON, under whose direction the work was carried out, and to Dr. E. G. ANDERSON, for suggestions and help rendered during the investigations.

EXPERIMENTAL RESULTS

Intercrosses

Experiments with white seedlings were begun in the spring of 1920. A few intercrosses were made in the summer of the same year, and a few more the next summer. It was not until the summer of 1922 that the intensive work was begun.

Up to this time, twenty-nine different intercrosses have been made between heterozygous plants of eighteen different stocks. The intercrosses between stocks which have genetically the same white seedling should segregate white in F_1. Contrary to expectation, all F_1 plants of the great majority of these intercrosses were green. In three cases only, the F_1 generation segregated white seedlings. In one of these cases the F_2 generation showed that the intercrossed stocks differed in their genetic constitution with respect to white seedling. In this cross three factors for white seedlings were present. The other two intercrosses were not carried farther than F_1.

These results indicate that the white phenotype in maize may be determined by many different factors. How many there are in the available material can be determined only by further investigations. At present, intercrosses are complete enough to show the presence of seven factors, and only one intercross is lacking to complete the test with another one.

The following table shows the stocks between which intercrosses were made and the F_1 seedlings found to be green (table 1.) The individuals used in each cross were selfed and shown to be heterozygous.

TABLE 1

STOCK NUMBER	1	2	3	8	11
1		x	x	x	x
2	x		x	–	x
3	x	x		x	x
8	x	–	x		x
11	x	x	x	x	

All the possible intercrosses except 2×8 were obtained. That these stocks were genetically different, however, may be inferred from the fact that the white phenotype occurring in stock 8 is determined by duplicate genes, while the white phenotype which is isolated from stock 2 is, as far as known, a simple Mendelian recessive.

Stock 4 has been intercrossed with stocks 1 and 2 only. In both cases the F_1 was green. From the cross 2×4 the F_2 generation was grown and found to give green and white seedlings in a 9 : 7 ratio, showing that two factors were involved. That white seedling in stock 4 is genetically different from that in stock 11 may be inferred from the fact that white seedling in stock 11 shows linkage with white endosperm (table 38, appendix), while white seedling in stock 4 does not show such a linkage (table 33). As far as known, the white phenotype in stock 4 is a simple Mendelian recessive and that in stock 8 is determined by duplicate genes. This fact makes it probable that white seedlings in stocks 4 and 8 are genetically different. Nothing is known about the relation between white seedlings in stocks 3 and 4. Cross 3×4 would show whether seven or eight factors for white seedlings were present in the stocks discussed.

Up to this time it has been possible to grow F_2 generations from three intercrosses between stocks 1, 2, 3, 8 and 11. Segregation in the F_2 generation (tables 28, 36 and 38) shows that white seedlings in these stocks are genetically different. From the other six intercrosses only the F_1 generation was grown. All the F_1 seedlings tested were green, however, which is possible only if the parents differ in their genetical constitution for white seedlings. To complete the test, it is necessary to grow the F_2 generation. It is considered, however, that the evidence presented may warrant the preliminary conclusion that the white phenotypes in stocks 1, 2, 3, 8 and 11 are determined by different genes. In stocks 1, 2 and 3 white seedling is a simple Mendelian recessive; therefore, in each case one gene is involved. For the expression of white seedling in stocks 8 and 11 duplicate genes are necessary.

The following symbols will be used for white seedlings:

w_3 for the gene for white seedling in stock 1
w_4 for the gene for white seedling in stock 2
w_5 for one of the duplicate genes in stock 11
w_6 for the other duplicate gene in stock 11
w_7 for the gene for white seedling in stock 3
w_8 for one of the duplicate genes in stock 8
w_9 for the other duplicate gene in stock 8

Genotype w_3 w_3

W_3 w_3 is the name for the gene which is responsible for the white seedling in stock 1. This white seedling is probably the one which LINDSTROM (1918) used in his studies on chlorophyll inheritance.

Results of numerous crosses (tables 30, 31, and 32) show that w_3 in the homozygous recessive condition was in every case sufficient for the expression of white phenotype.

Cross between stocks 3 and 1

Table 28 gives the F_2 data of the cross between stocks 3 and 1. Four ears segregated in a 9 : 7 ratio, giving a total of 649 green and 490 white seedlings. The calculated numbers are 640.7 green and 498.3 white, giving a deviation from expectancy of 8.3 ± 11.3. The fit is very close, and the conclusion is justified that in this cross two independent genes were present, each producing the white phenotype when homozygous recessive. Four ears segregated in the 3 : 1 ratio with a total of 1012 green and 315 white seedlings. The deviation from the calculated numbers is 16.75 ± 10.6. One ear gave green seedlings only.

Heterogeneity of the F_1 plants which is expressed in the F_2 progenies is a result of the heterozygous condition of the parents. It is supposed that the parent plants had the following genetic constitution regarding white seedlings:

♀ parent, $W_3\ W_3\ W_7\ w_7$
♂ parent, $W_3\ w_3\ W_7\ W_7$

The frequency of F_1 plants was:

TABLE 2

PROGENIES SEGREGATING IN.....	9 : 7	3 : 1	GREEN
Observed.....	4	4	1
Calculated.....	*2.25*	*4.5*	*2.25*
Difference.....	+1.75	−.5	−1.25

$\chi^2 = 2.11$, $P = .352$

The fit is reasonably close.

Cross between stocks 6 and 1

The F_2 generation grown from the cross between stocks 6 and 1 shows a few interesting points. By an examination of table 29 it can be seen that the F_1 plants were of four kinds. Three of them gave only green progeny; four segregated in the 3 : 1 ratio; one segregated in the 9 : 7 ratio, giving 129 green and 94 white seedlings with a difference from expectancy of 4.0 ± 5.0; and one segregated in the 15 : 1 ratio, giving 216 green and 16 white seedlings with a difference of 1.8 ± 2.48.

The ratios obtained in F_2 are an expression of a recombination of three different factors for white seedling. The 15 : 1 ratio indicates that two of these factors act as duplicate genes producing white seedling in the double recessive condition only. Both of these factors were brought into the cross by the parent from stock 6. This conclusion may be drawn from the fact that progenies of certain plants in stock 6 segregated in the 15 : 1 ratio.

A 9 : 7 ratio would be expected in the F_2 generation of this cross only in case stock 1 had the recessive allelomorphs of two genes. One of these genes was w_3, which, as far as known, is sufficient in itself to produce the white phenotype when homozygous recessive. The other gene was one of the duplicate genes present in stock 6. The duplicate genes from stock 6 are not named as yet, because it is not known whether they differ from the duplicate genes $W_8\ w_8$ and $W_9\ w_9$. They will temporarily be called $W_b\ w_b$ and $W_c\ w_c$.

Frequencies of F_1-generation plants indicate that the parent plants probably had the following genetical constitution for white seedling:

♀ parent from stock 6 = $W_3\ W_3\ W_b\ w_b\ W_c\ w_c$

♂ parent from stock 1 = $W_3\ w_3\ W_b\ w_b\ W_c\ W_c$; $W_3\ w_3\ W_b\ W_b\ W_c\ w_c$ $W_3\ w_3\ W_b\ W_b\ w_c\ w_c$ or $W_3\ w_3\ w_b\ w_b\ W_c\ W_c$

The frequencies of F_1 plants are as follows (table 3):

TABLE 3

PROGENIES SEGREGATING IN	9 : 7	3 : 1	45 : 19	15 : 1	GREEN
Observed.....	1	4	0	1	3
Calculated, ♂ = $W_3\ w_3\ W_b\ w_b\ W_c\ W_c$.....	*.56*	*3.38*	*1.12*	*1.12*	*2.82*
Difference.....	+.44	+.62	−1.12	−.12	+.18

The fit is very close, χ^2 equaling 1.608 and P = .803. When the calculation is made on the other possibility, e.g., on the assumption that the male parent had the genetical constitution, $W_3\ w_3\ W_b\ W_b\ w_c\ w_c$ or $W_3\ w_3\ w_b\ w_b\ W_c\ W_c$ then $\chi^2 = 1.518$ and P = .82. The fit would be very poor if the parent plants used in the cross had any other genetical constitution than noted above. One class of plants which would give an F_2 progeny segregating in 45 : 19 ratio, was not detected. This ratio would be obtained by selfing a plant which was heterozygous for all three factors for white. The small number of plants grown may account for that deficiency.

Crosses for linkage

It is not possible to make back-crosses with white seedlings, and therefore conclusions about linkage have to be drawn from the F_2 data.

Characters which can be detected in seeds or seedlings are the best ones for testing linkage relations, and especially so when a lethal factor like the white seedling is being tested. Gene w_3 has been tested for linkage with shrunken endosperm (s_h); one of the factors for aleurone color (R); liguleless (l_g); dwarf plants (d); and the factor for purple aleurone (P_r).

TEST OF w_3-s_h. Several crosses were made between plants of the constitution $W_3\,W_3\,S_h\,S_h \times W_3\,w_3\,s_h\,s_h$. In the case of linkage, when F_2 data are used, the divergence from the expectancy in recombination classes is much larger in the coupling than in the repulsion series.

Table 30 gives the data of the above-mentioned cross. The summary appears in table 4.

TABLE 4

	$S_h\,W_3$	$S_h\,w_3$	$s_h\,W_3$	$s_h\,w_3$	TOTAL
Observed	1822	582	511	182	3097
Calculated	*1742.10*	*580.66*	*580.66*	*193.58*	
Difference	+79.90	+1.34	−69.66	−11.58	

$\chi^2 = 12.718$, P = .0054

The fit is very poor. There are only about five chances in a thousand that the observed deviation is due to errors of random sampling. That the observed deviation is not due to the linkage between w_3 and s_h can be seen from the fact that the parental class $s_h\,w_3$ is smaller and the recombination class $S_h\,w_3$ larger than the calculated numbers on the non-linkage basis. Furthermore, if we compare the ratios between green and white seedlings in S_h and in s_h classes separately, the deviation from expectancy is very small (table 5).

TABLE 5

	$S_h\,W_3$	$S_h\,w_3$	$s_h\,W_3$	$s_h\,w_3$
Observed	1822	582	511	182
Calculated	*1803*	*601*	*518.75*	*174.25*
Difference	+19±14.3		−7.75±7.69	

All this evidence shows that there is no close linkage between s_h and w_3.

A comparison of germination of S_h and s_h seed indicates that the large observed deviation from expectancy, when the four classes are considered together, may be due to the poorer germination of the shrunken seed.

In the S_h class, 93.28 percent of planted seeds produced seedlings and in the s_h class 80.68 percent only. When a correction is made for the low germination of the s_h seeds the comparison is as follows (table 6):

TABLE 6

	$S_h W_3$	$S_h w_3$	$s_h W_3$	$s_h w_3$	TOTAL
Corrected	1822	582	590.87	210.44	3205.31
Calculated	*1802.99*	*600.99*	*600.99*	*200.34*	
Difference	+19.01	−18.99	−10.12	+10.10	

The fit is very close, χ^2 equaling 1.479 and P = .693, which is another confirmation of the assumption that no close correlation between s_h and w_3 exists.

TEST OF w_3-l_g. In table 31 are arranged the F_2 data obtained from the cross $R\ l_g\ d\ W_3 \times r\ L_g\ D\ W_3\ w_3$ from which the linkage relation between w_3 and l_g, r and d can be studied. The data on the relation of w_3 and l_g can be summarized as in table 7.

TABLE 7

	$L_g W_3$	$L_g w_3$	$l_g W_3$	$l_g w_3$	TOTAL
Observed	515	155	184	72	926
Calculated	*520.9*	*173.6*	*173.6*	*57.9*	
Difference	−5.9	−18.6	+10.4	+14.1	

The fit is fairly close, χ^2 being 6.116 and P = .107. The observed deviation is larger than it would be otherwise, since the separation into classes was made too early, and probably too many plants were classified as liguleless. Still the fit is close enough to warrant the conclusion that no appreciable linkage exists between l_g and w_3.

TEST OF w_3-r. The data concerning the relation between w_3 and the r factor for the color of the aleurone are to be found in tables 31 and 32, summarized in table 8.

TABLE 8

	$R W_3$	$R w_3$	$r W_3$	$r w_3$	TOTAL
Pedigree 13 (table 32)	712	234	247	102	1295
Pedigree 15 (table 31)	1081	343	334	102	1860
Total	1793	577	581	204	3155
Calculated	*1777*	*592.3*	*592.3*	*197.4*	
Difference	+16	−15.3	−11.3	+6.6	

The fit is very close, χ^2 equaling .983 and P > .80, so that the conclusion is justified that w_3 and r are not closely linked.

TEST OF w_3-d. Table 31 gives the data on the relation between w_3 and the factor d for dwarfness. The summary is given in table 9.

TABLE 9

	$D\,W_3$	$D\,w_3$	$d\,W_3$	$d\,w_3$	TOTAL
Observed	362	100	109	35	606
Calculated	*340.9*	*113.6*	*113.6*	*37.9*	
Difference	+21.1	−13.6	−4.6	−2.9	

The fit is close enough, χ^2 equaling 3.34 and P = .347, indicating no close relation between w_3 and d.

TEST OF w_3-p_r. A summary of the data from table 32 is given in table 10.

TABLE 10

	$P_r\,W_3$	$P_r\,w_3$	$p_r\,W_3$	$p_r\,w_3$	TOTAL
Observed	207	64	67	24	362
Calculated	*203.6*	*67.9*	*67.9*	*22.6*	
Difference	+3.4	−3.9	−.9	+1.4	

The fit is very close, χ^2 being .3897 and P larger than .80. The conclusion is warranted that no close linkage exists between w_3 and p_r.

Genotype w_4 w_4

The stock carrying the recessive factor w_4 was derived from a plant of Howling Mob sweet corn grown by Doctor ANDERSON as a sample of pseudo-starchy endosperm. All selfed plants which were used in intercrosses segregated white seedling in a 3 : 1 ratio. This stock was extensively used in intercrosses with the other stocks, because it had sugary endosperm.

Cross between stocks 2 and 4

The cross between stocks 2 and 4 gave a green F_1 generation and segregated in the F_2 generation in a 9 : 7 ratio.

Parent plants used in the cross were heterozygous for the white seedling. From the selfed seed of the female parent (No. 10–1) 18 green and 7 white seedlings were obtained and from the selfed seed of the male parent 30 green and 10 white seedlings. All the tests gave green seedlings in F_1.

Table 33 gives the F_2 data of this cross. The progenies from three selfed F_1 ears segregated into 3 : 1 ratios with a total of 742 green and 231 white seedlings, the difference from the expectancy being 12.25 ± 9.11. The progenies from the other three ears segregated into 9 : 7 ratios, having a total of 391 green and 285 white seedlings. The difference from expectancy is 10.75 ± 8.7. Three ears had green progenies only.

The F_2 data show conclusively that in this cross two independent factors for the white phenotype were present. They were brought into the cross one by each parent. Presumably the parents had the following genetical constitution regarding white seedlings: $W_4\, w_4\, W_a\, W_a \times W_4\, W_4\, W_a\, w_a$.[4] The frequencies of F_1 plants support that assumption (table 11.)

TABLE 11

PROGENIES SEGREGATING IN.....	9 : 7	3 : 1	GREEN	TOTAL
Observed.....	3	3	3	9
Calculated.....	*2.25*	*4.5*	*2.25*	
Difference.....	+.75	−1.5	+.75	

$\chi^2 = .91$; $P > .606$

The F_3 generation was grown from four F_2 ears. Three of these ears segregated in a 9 : 7 ratio and one in a 3 : 1 ratio. Table 34 gives the F_3 data. The F_2 plants grown from 9 : 7 ears were as follows (table 12):

TABLE 12

PROGENIES SEGREGATING IN.....	9 : 7	3 : 1	GREEN	TOTAL
Observed.....	6	4	2	12
Calculated.....	*5.3*	*5.3*	*1.4*	
Difference.....	+.7	−1.3	+.6	

$\chi^2 = .44$, $P > .606$

Selfed plants grown from the seed taken from the 3 : 1 ear (pedigree 797) gave two kinds of progenies; i.e., green ones and others segregating into a 3 : 1 ratio, just as was expected.

Linkage relations

With w_4 no special crosses for linkage were made. Parent plants, however, used in the cross between stocks 2 and 4 differed in their genetical

[4] The relation between established genes for white seedlings and the gene for albinism which is present in stock 4 is not known. The symbol $W_a\, w_a$ will be used in this chapter as a name for the gene from stock 4.

constitution for endosperm, and the result was that the F_2 generation segregated for endosperm characters also. Seeds differing in endosperm were planted separately and notes on white seedlings taken. From the data obtained, conclusions may be drawn on linkage relations between w_4, w_a, and s_u, y, and y_p, which factors were involved in the cross. As far as was noted, the parents had the following genetical constitution:

♀ parent 10–1 $s_u\ y\ y_p\ W_4\ w_4\ W_a\ W_a$

♂ parent 6–9 $= S_u\ Y\ Y_p\ W_4\ W_4\ W_a\ w_a$

The F_1 plants differed in genetical constitution for white seedling. This difference was best expressed on the segregation of their progenies. Some of them segregated for white seedlings in a 3 : 1 ratio, indicating that they were heterozygous for one of the factors for white. Theoretically the progeny of half of the plants should segregate $w_4\ w_4$ and the other half $w_a\ w_a$. But there is no way of differentiating between the two genotypes other than by later breeding tests. If linkage between either of them and any of the involved endosperm factors existed, they could be separated because of the fact that in the case of w_4 there would be a coupling, and in the case of w_a a repulsion relation. White seedlings segregated from the progenies of part of the F_1 plants in a 9 : 7 ratio, indicating the presence of both of the factors for white seedling. If reasonably close linkage existed between either of them and any of the factors for endosperm that were involved, it would have been detected in spite of the fact that the 9 : 7 ratio is not favorable for the expression of linkage.

TEST OF w_4-w_a-s_u. A summary of data from progenies of the plants which segregated in a 3 : 1 ratio is given in table 13.

TABLE 13

PEDIGREE NUMBER		$S_u\ W$	$S_u\ w$	$s_u\ W$	$s_u\ w$	TOTAL	GOODNESS OF FIT
332–1	Observed.....	193	49	54	17	313	
	Calculated.....	*176.1*	*58.7*	*58.7*	*19.5*		$\chi^2=3.92$
	Difference.....	+16.9	−9.7	−4.7	−2.5		P= .27
332–7	Observed.....	150	48	42	16	256	
	Calculated.....	*144*	*48*	*48*	*16*		$\chi^2=1.00$
	Difference.....	+6	0	−6	0		P= .80
332–8	Observed.....	127	49	45	13	234	
	Calculated.....	*131.6*	*43.9*	*43.9*	*14.6*		$\chi^2=.883$
	Difference.....	−4.6	+5.1	+1.1	−1.6		P>.80

The following are the data on the progenies from plants segregating in a 9 : 7 ratio (table 14):

TABLE 14

	$S_u\,W$	$S_u\,w$	$s_u\,W$	$s_u\,w$	TOTAL
Observed	282	198	75	56	611
Calculated	*258*	*201*	*85.5*	*66.5*	
Difference	+24	−3	−10.5	−10.5	

$\chi^2=6.229$, P = .103

The fit would be still better if it were not for the low germination of the sugary classes.

The only conclusion that can be made from the above data is that no close linkage exists between sugary endosperm and either w_4 or w_a.

TEST OF w_4-w_a-y. Data relating to the progenies of the plants which segregate into a 3 : 1 ratio are given in table 15.

TABLE 15

PEDIGREE NUMBER		YW	Yw	yW	$y\,w$	TOTAL	GOODNESS OF FIT
322–1	Observed	146	34	47	15	242	
	Calculated	*136.1*	*45.4*	*45.4*	*15.1*		$\chi^2=3.537$
	Difference	+9.9	−11.4	+1.6	−.1		P = .338
332–7	Observed	111	35	39	13	198	
	Calculated	*111.4*	*37.1*	*37.1*	*12.4*		χ^2 = .25
	Difference	−.4	−2.1	+1.9	+.6		P > .80
332–8	Observed	97	37	33	12	179	
	Calculated	*100.8*	*33.5*	*33.5*	*11.2*		χ^2 = .578
	Difference	−3.8	+3.5	−.5	+.8		P > .80

The data of 9 : 7 families are summarized in table 16.

TABLE 16

	$Y\,W$	$Y\,w$	$y\,W$	$y\,w$	TOTAL
Observed	200	160	72	48	480
Calculated	*202.5*	*157.5*	*67.5*	*52.5*	
Difference	−2.5	+2.5	+4.5	−4.5	

$\chi^2=.76$ P > .80

In all the cases the fit is very close and the conclusion that there is no close linkage between w_4, w_a and y is justifiable.

TEST OF w_4-w_a-y_p. A summary of the data is given in table 17.

TABLE 17

PEDIGREE NUMBER		Y $W_4^?$	Y w	y W	y w	TOTAL	GOODNESS OF FIT
332–1	Observed.....	35	12	12	3	62	
	Calculated.....	*34.9*	*11.6*	*11.6*	*3.9*		χ^2=.232 P>.80
	Difference.....	+.1	+.4	+.4	−.9		
332–7	Observed.....	30	11	9	2	52	
	Calculated.....	*29.25*	*9.75*	*9.75*	*3.25*		χ^2=.719 P>.80
	Difference.....	+.75	+1.25	−.75	−1.25		
332–8	Observed.....	24	10	9	2	45	
	Calculated.....	*25.4*	*8.4*	*8.4*	*2.8*		χ^2=.654 P>.80
	Difference.....	−1.4	+1.6	+.6	−.8		

The data of 9 : 7 families are shown in table 18.

TABLE 18

	Y W	Y w	y W	y w	TOTAL
Observed.....	60	36	22	12	130
Calculated.....	*54.8*	*42.7*	*18.3*	*14.2*	
Difference.....	+5.2	−6.7	+3.7	−2.2	

χ^2=2.64 P>.457

The numbers are not very large, but in each case the fit is very close, and the conclusion may be drawn that there is no linkage between w_4, w_a, and the factor for the pale yellow endosperm.

Cross between stocks 6 and 2

The progeny of the female parent from stock 6 segregated in a 15 : 1 ratio, giving 70 green and 6 white seedlings with a deviation from expectancy of 1.0 ± 1.42. The male parent from stock 2 produced green and white seedlings in a 3 : 1 ratio. All the F_1 seedlings of the cross 6×2 were green, indicating that the white seedlings involved in the parent stocks were genetically different. Table 35 gives the F_2 data.

From the table it can be seen that two pedigrees segregated in a 63 : 1 ratio with a total of 196 green and 5 white seedlings, the deviation

from expectancy being only 1.86 ± 1.19. Two other pedigrees segregated into a 15 : 1 ratio, having a total of 180 green and 11 white seedlings, with a difference from expectancy of $.94 \pm 2.26$. Two pedigrees segregated in a 3 : 1 ratio, and the last two gave green seedlings only. Segregation in a 63 : 1 ratio shows that three homozygous recessive genes were necessary for the expression of the white seedling in question. A 15 : 1 ratio is a result of a recombination of these three genes.

The segregation of progenies from the selfed parent plants together with the frequencies of the F_1 plants indicates that the genetic constitution of the parent was as follows:

♀ parent from stock 6 = $W_4\ W_4\ W_b\ w_b\ W_c\ w_c\ w_d\ w_d$[5]

♂ parent from stock 2 = $W_4\ w_4\ w_b\ w_b\ W_c\ W_c\ W_d\ W_d$

A comparison follows (table 19):

TABLE 19

PROGENIES SEGREGATING IN	3 : 1	15 : 1	45 : 19	63 : 1	GREEN
Observed.....	2	2	0	2	2
Calculated.....	*3*	*1*	*1*	*1*	*2*
Difference.....	−1	+1	−1	+1	0

$\chi^2 = 3.33$ P = .507

The numbers were small, which probably accounts for the fact that not all expected classes have been detected.

Genotypes $w_5\ w_5$ and $w_6\ w_6$

The origin of stock 11, carrying recessive factors w_5 and w_6, was an ear of dent corn No. 1975–2 taken from the cultures of Doctor ANDERSON.

The data on the progenies of selfed plants which are segregating white seedlings may be found in table 37. In spite of the fact that the numbers are very small, it can be seen that the segregation is very irregular and that probably more than one factor is necessary for the expression of the white phenotype.

Cross between stocks 11 and 3

A cross between stocks 11 and 3 gave the most interesting F_2 data of all the crosses reported in this paper. All plants of the F_1 generation were green. Table 38 presents the F_2 data.

[5] $w_b\ w_c\ w_d$ are symbols used in this chapter only to indicate genes for white seedling from stock 6.

LINKAGE BETWEEN w_5 AND y. The female parent from stock 11 had white endosperm and the male parent from stock 3 had yellow endosperm. The F_2 seed was separated according to the endosperm color, and each class planted separately. From the data in table 38 it may be noted that in certain pedigrees a definite correlation exists between white seedlings and white color of endosperm. The pedigrees which segregate white seedlings in a 3 : 1 ratio are the best to be used for the determination of linkage. The data are given in table 20.

TABLE 20

PEDIGREE NUMBER	*Y W*	*Y w*	*y W*	*y w*	TOTAL	GOODNESS OF FIT
803–7	86	23	13	18		
–9	164	14	22	36		
Observed	250	37	35	54	376	
Calculated (without linkage)	*211.5*	*70.5*	*70.5*	*23.5*		
Difference	+38.5	−33.5	−35.5	+30.5		$\chi^2=71.5$ $P<10^{-6}$
Calculated (with linkage and 24.3 percent crossing over)	*242.2*	*39.9*	*39.9*	*54*		
Difference	+7.8	−2.9	−4.9	0		$\chi^2=1.065$ $P=.7864$

From the comparison made above it can be seen that when the calculations are made on the basis of a free segregation of factors, the chances are exceedingly low that the observed deviation from expectancy may be due to errors of random sampling. On the contrary, the fit is very close if calculations are made with the assumption of linkage and the conclusion is warranted that the linkage between the factor for white seedling and that for white endosperm exists. From the data obtained the percentage of crossing over is computed by EMERSON'S (1916) formulae to be 24.3.

Since the data in question represents the coupling series it can be seen that the linked factor for white seedling must have come from the female parent which carried the factor for white endosperm.

KEMPTON (1917) made a preliminary report on a case of linkage between white seedling and white endosperm. Intercrosses between his white seedling and the one used in this investigation have not been made as yet.. The data presented by KEMPTON, owing to the complexity of the case, were not satisfactory for the calculation of percentage of crossovers, which fact makes an indirect check impossible.

FREE SEGREGATION BETWEEN w_7 AND y. The recessive gene w_7 was brought into the cross by the male parent. The white seedling, which does not show linkage with white endosperm, and is found in pedigrees which segregate in a 3 : 1 ratio, is determined by w_7. The relation between w_7 and endosperm color may be seen from the following summary of the data (table 21):

TABLE 21

	Y W	*Y w*	*y W*	*y w*	TOTAL
Observed	328	91	111	25	555
Calculated	*312.75*	*103.75*	*103.75*	*34.75*	
Difference	+15.25	−12.75	+7.25	−9.75	

The fit is fairly close, χ^2 being 5.57 and P = .1376, and the conclusion may be drawn that no close linkage between w_7 and y exists.

A 9 : 1 RATIO. From table 38 it can be seen that in three pedigrees white seedlings segregated in almost exactly a 9 : 1 ratio. The repeated occurrence of a ratio very close to 9 : 1 suggests that this ratio could hardly be attributed to deviations from other ratios, due entirely to errors of random sampling. The only simple ratio which is close enough to 9 : 1 to be considered is the 15 : 1 ratio.

The following is a summary of the data of pedigree 801–3, 802–2, and 803–13 which segregated in a 9 : 1 ratio (table 22):

TABLE 22

SEEDLINGS	*W*	*w*	TOTAL
Observed	409	45	454
Calculated (15 : 1)	*425.6*	*28.4*	
Difference	−16.6±3.48		

The deviation from the expectancy is 4.8 times its probable error, and the chance that the observed difference is due to errors of random sampling is about one in a thousand. The probability is much too low to support the conclusion that in the given case 15 : 1 was the expected ratio.

The 9 : 1 ratio, however, could be a modified 15 : 1 ratio. This modification may be due to linkage of duplicate genes. Coupling between two duplicate genes would tend to make the ratio smaller. The ratio may be modified between the limits of 15 : 1 and 3 : 1 according to the close-

ness of linkage. On the contrary, repulsion between the two duplicate genes would tend to increase the ratio between the limits of 15 : 1 and 1 : 0.

It is assumed that the 9 : 1 ratio observed in the cross 11×3 is caused by coupling between two duplicate genes with about 36.9 percent of crossing over between them.

LINKAGE WITH ENDOSPERM COLOR. The data from pedigrees which segregate in a 9 : 1 ratio show coupling between white seedling and white endosperm. This linkage relation is a good check of the assumption that linked duplicate genes are involved in the cross.

If the above assumption be correct, then the observed classes are a product of a recombination of three linked genes, i.e., two duplicate genes for white seedling and one for the color of endosperm. If calculations made on that basis agree with the observed data, this is another strong support of the hypothesis.

As shown before, about 24.3 percent of crossovers occur between the gene y for endosperm color and w_5 one of the duplicate genes for white seedling. The percentage of crossovers between w_5 and w_6 is about 36.9. There are two possibilities with respect to the order of these three linked genes. The order may be Y-W_5-W_6 or W_5-Y-W_6. The possibility of its being W_5-W_6-Y is eliminated by the fact that the percentage of crossing over between W_5-W_6 is larger than that between W_5-Y.

To determine which was the probable order of the genes in the given case, both possibilities are tried out in the calculations.

The formulae for the calculation of frequencies of different classes are developed on the same principle as used by EMERSON (1916). They are as follows:

The frequency for the class with:

Yellow endosperm and green seedlings $= 3a^2+4ab+6ac+6ad+6bc+6bd+2b^2+3c^2+6cd+3d^2$

Yellow endosperm and white seedlings $= 2ab+b^2$

White endosperm and green seedlings $= 2ab+b^2+2ac+2bc+c^2+2ad+2bd+2cd+d^2$

White endosperm and white seedlings $= a^2$

When it is assumed that the order of the genes is Y-W_5-W_6, then,
a stands for the frequency of non-crossovers;
b stands for the frequency of single crossovers in region Y-W_5;
c stands for the frequency of single crossovers in region W_5-W_6;
d stands for the frequency of double crossovers.

The value of d is computed indirectly from the theoretical formula: $\frac{(b+d)\ (c+d)}{100} = d$, the interference not being taken into account.

When it is assumed that the order of the genes is W_5-Y-W_6, then,
a stands for the frequency of non-crossovers;
b stands for the frequency of double crossovers;
c stands for the frequency of single crossovers in region Y-W_6;
d stands for the frequency of single crossovers in region W_5-Y.

Then the values for a, b, c and d are calculated as follows:

$$d+c=36.9$$
$$d+b=24.3$$
$$b=\frac{24.3\times(b+c)}{100}$$

A comparison of the two possibilities is made in (table 23).

TABLE 23

PEDIGREE NUMBER		*Y W*	*Y w*	*y W*	*y w*	TOTAL	GOODNESS OF FIT
801–3		125	3	13	12		
802–2		125	5	28	12		
803–13		99	4	19	9		
	Observed	349	12	60	33	454	
	Calculated (Y-W_5-W_6	*320*	*19.2*	*88.8*	*26*		
	Difference	+29	−7.2	−28.8	+7		$\chi^2=16.56$ P = .000752
	Calculated (W_5-Y-W_6	*332.5*	*8.1*	*76.5*	*36.9*		
	Difference	+16.5	+3.9	−16.5	−3.9		$\chi^2=6.662$ P = .0854

The possibility that the order of the genes was Y-W_5-W_6 is practically eliminated by the very poor fit between observed and calculated data. The chances that the observed deviation is due to the errors of random sampling are about 7.5 in ten thousand.

On the other hand, a satisfactory fit supports the possibility that the order of the genes is W_5-Y-W_6. The fit would be still closer if it were not for the low germination of classes with white endosperm in pedigree No. 801–3. The germination of yellow seeds was 75 percent and white ones 45.5 percent only. This poorer germination of white seed does not appreciably change the ratio between green and white seedlings but

makes the classes with white endosperm lower. This is very clearly indicated in deviations from expectancy which are minus for both of the white-endosperm classes. If pedigree No. 801–3 is disregarded and No. 802–2 and No. 803–13 only taken into account, the fit is very close, χ^2 being 3.3057 and P = .3518.

The conclusion that the order of the genes is W_5-Y-W_6 may also be drawn from other evidence. When the observed values for different classes are substituted in the formulae mentioned above, four equations are obtained which can be solved for a, b, c and d. The values obtained in that way are as follows: $a = 5.745$, $b = .965$, $c = 1.415$, $d = 2.375$. The relative values of b and d are of significance for the conclusion. It will be recalled that b stands for double crossovers when the order of the genes is W_5-Y-W_6, and for single crossovers between Y-W_5 when the order is assumed to be Y-W_5-W_6. Similarly, d stands for double crossovers if the order is Y-W_5-W_6 and for single crossovers in the region W_5-Y if the order is W_5-Y-W_6. The relative value of b as obtained by calculation shows that it can be the frequency of double crossovers only, and therefore proves that the order of the genes is W_5-Y-W_6.

Y is about half way between W_5 and W_6. The percentage of crossing over between W_5 and Y is about 24.3 and between Y and W_6 about 24.5. P_l, one of the factors for the plant color, was shown to be linked with Y (EMERSON 1921, ANDERSON 1921). A cross involving all of these four factors should give more satisfactory data on the percentage of crossovers, but as yet it has not been grown.

A 28.6 : 1 RATIO. As shown before in the case of coupling between linked duplicate genes, when the percentage of crossovers is 36.9, the expected ratio of green to white seedlings will be 9 : 1. On the contrary, the expected ratio will be 28.6 : 1 in the case of repulsion between the duplicate genes, with the same percentage of crossing over. Pedigree No. 803–15 segregated in 84 green seedlings and 1 white with a deviation from the 28.6 : 1 ratio of 1.86 ± 1.1. It is not considered, however, that one white seedling is sufficient evidence for a conclusion. It may be only an accident due to error or to some unknown cause. During the work with the other seedling characters in a few instances there were observed single white seedlings in pedigrees which otherwise did not throw white. The probability is very high, however, that the deviation from the expectancy in this case is due to errors of random sampling. The F_3 generation will be necessary for a final conclusion.

A 9 : 7 OR 2.08 : 1 RATIO. From the data which are now available it is not possible to determine exactly into which ratio pedigrees 803–10,

803–17, and 803–18 segregated. There are two ratios possible, i.e., 9 : 7 and 2.08 : 1, the latter being a combination of 3 : 1 and 9 : 1 ratios. They are too close to be distinguished with numbers of individuals obtained hitherto.

A 9 : 7 ratio would occur if the parent plants were homozygous recessive for one of the duplicate genes and heterozygous for the other one and also for w_7. A 2.08 : 1 ratio would result from heterozygosity of all three genes, i.e., w_7, w_5 and w_6. In both cases linkage between white seedling and white endosperm should be evident. The two possibilities are compared in table 24.

TABLE 24

	Y W	*Y w*	*y W*	*y w*	TOTAL	GOODNESS OF FIT
Observed (803-10, -17, -18)..	189	89	37	44	359	
Calculated (9 : 7).....	*174*	*96.3*	*28.7*	*60*		
Difference.....	+15	−7.3	+8.3	−16		χ^2=8.48 P= .0425
Calculated (2.08 : 1).....	*194*	*73.6*	*46.4*	*45*		
Difference.....	−5	+15.4	−9.4	−1		χ^2=5.262 P= .1561

The data of the F_3 generation are needed for a final conclusion.

GENETICAL CONSTITUTION OF F_1 PLANTS. The unknown parts of the genetical constitution of parents may be determined from the frequency of occurrence of the several kinds of F_2 behavior. The most probable constitutions of the parents are:

♀ parent from stock 11 = *y y* W_7 W_7 W_5 w_5 W_6 w_6

♂ parent from stock 3 = *Y Y* W_7 w_7 W_5 W_5 W_6 w_6

A comparison follows (table 25):

TABLE 25

SEGREGATION IN F_2.....	9 : 7 AND 2.08 : 1	3 : 1 WITHOUT LINKAGE	3 : 1 LINKAGE WITH *y*	9 : 1	28.6 : 1	GREEN
Observed.....	3	7	2	3	1	3
Calculated.....	*3*	*6.5*	*1.5*	*1.5*	*.87*	*5.63*
Difference.....	0	+.5	+.5	+1.5	+.13	−2.63

The fit is very close, χ^2 being 2.949 and P = .708.

SUMMARY OF RESULTS OF THE CROSS 11 AND 3. The F_2 data from the cross of the stocks 11 and 3 indicate the presence of linked duplicate genes. This indication is supported by:

1. The repeated occurrence of segregation in very close to a 9 : 1 ratio, which is assumed to result from coupled duplicate genes when 36.9 percent of crossing over takes place.
2. The occurrence of a 28.5 : 1 ratio, which is supposed to be the result of repulsion between duplicate genes, with 36.9 percent of crossing over. This point, however, has to be tested in the F_3 generation.
3. A satisfactory fit between observed and calculated data, when linkage between duplicate genes is used as a basis for calculations.
4. A very close fit between observed and calculated frequencies of F_1 plants giving the several kinds of segregation in F_2.

For a final conclusion, however, the F_3 data are necessary.

The F_2 data show the existence of linkage between endosperm color and white seedling which is determined by the linked duplicate genes. A reasonable fit between observed and calculated data was obtained when the calculations were made on the assumption that the order of the genes was W_5-Y-W_6, with about 25 percent of crossing over in each region.

It was shown also that white seedlings brought into the cross by different parents were genetically different.

Genotype w_7 w_7

The stock carrying the recessive factor w_7 originated from a selfed ear grown by Doctor D. F. JONES, and sent to Doctor E. G. ANDERSON for a study of its very deep orange endosperm color.

All crosses and selfings made up to this time show that w_7 in homozygous recessive condition is sufficient for the expression of the white phenotype.

Cross between stocks 8 and 3

Table 36 gives the F_2 data from a cross between stocks 8 and 3. From the table it can be noticed that in the pedigrees 800–4, –6, and –13, the deviation from the expectancy is too large to be due to errors of random sampling. It is thought that this large deviation is caused by the fact that in the same pedigrees there was present a weak morphological character called "spear" which made the classification of white seedlings very difficult.

The progenies of the F_1 plants segregated in 15 : 1, 3 : 1, 9 : 7, and 45 : 19 ratios. A 45 : 19 ratio was obtained from No. 805–5, which gave 339 green and 155 white seedlings, with a difference from expectancy of

8.4 ± 6.85. A 45 : 19 ratio is not far from the 3 : 1 ratio. In the present case 31.5 ± 6.49 would be the deviation from expectancy calculated on a 3 : 1 basis. It would mean about one chance in a thousand that the observed deviation was due to random sampling. The fit is much closer if the calculation is made on the basis of a 45 : 19 ratio. In that case the chances are about four in ten that the observed deviation is due to random sampling.

Segregation into a 45 : 19 ratio shows that the selfed plant was heterozygous for three factors determining white seedlings, two of them being duplicate genes.

The frequencies of F_1 plants are as follows (table 26):

TABLE 26

PROGENIES SEGREGATING IN.....	9 : 7	3 : 1	15 : 1	45 : 19	GREEN
Observed.....	3	4	1	1	6
Calculated.....	*3.75*	*3.75*	*1.87*	*1.88*	*3.75*
Difference.....	−.75	+.25	−.87	−.88	+2.25

$\chi^2 = 2.33$ $P = .677$.

The expected numbers are calculated with the assumption that the parent plants had the following constitution:

♀ parent from stock $8 = W_7\ W_7\ W_8\ w_8\ W_9\ w_9$

♂ parent from stock $3 = W_7\ w_7\ W_8\ w_8\ W_9\ W_9$

or less probably

♀ parent from stock $8 = W_7\ W_7\ W_8\ w_8\ W_9\ W_9$

♂ parent from stock $3 = W_7\ w_7\ W_8\ w_8\ W_9\ w_9$

It is believed that one of these assumptions is correct. The F_2 data showed plainly that in the present cross three factors for white seedlings were involved, two of which are duplicate genes. The above parental combinations are the only ones which give in the F_1 generation a satisfactory fit with the data obtained.

Genotypes $w_8\ w_8$ and $w_9\ w_9$

White seedling which is determined by duplicate genes $w_8\ w_9$ was found in the selfed progenies of High Protein Strain of corn obtained from SOUTH DAKOTA EXPERIMENTAL STATION. The data which show the F_2 segregation can be found in table 36, and the discussion of the results is given on pages 582 and 583.

A 63 : 1 ratio

A cross was made between a plant heterozygous for white seedling from stock 5 and a normal green plant. The progeny of two F_1 plants segregated into a 63 : 1 ratio, and the progeny of four other plants were green. The data are given in table 27.

TABLE 27

PEDIGREE NUMBER	*W*		w
813–7	115		3
–8	147		5
Total	262		8
Calculated	*266.2*		*4.2*
Difference	−3.8	±	1.37

The segregation into the 63 : 1 ratio indicates that three recessive pairs of genes are required for the expression of this white seedling. A 63 : 1 ratio, however, may be a 15 : 1 ratio modified by a repulsion between duplicate genes. The F_3 generation will give the evidence for the final conclusion.

It is not known as yet if this white seedling is genetically different from the one described before, which was shown to be determined by triplicate genes.

SUMMARY

White seedlings, frequently found in the commercial varieties of maize, are determined by many genetically different factors.

The investigation is not as yet sufficiently complete to show how many factors for albinism were present in the material used in the tests. The analysis has advanced far enough to prove the existence of seven different genes for white seedlings, but indications are very strong that there are many more.

Three of these factors are single Mendelian recessives.

Two others are duplicate genes. The progeny of a selfed plant which is heterozygous for both of these genes segregates into a 15 : 1 ratio.

The remaining two factors are also duplicate genes. The indications are strong that they are linked together with about 36.9 percent of crossing over.

Segregation into a 63 : 1 ratio was observed among the progenies of two unrelated stocks. This ratio suggests the existence of triplicate genes.

The relation between these genes and those mentioned above is not known.

It was shown that w_3 is not closely linked with any one of the following: s_h, l_g, d, r and p_r.

Gene w_4 and the factor for white seedling in stock 4 are not closely linked with s_u, y and y_p.

Genes w_5 and w_6 are two duplicate genes linked together. They are also linked with endosperm color. The probable order of the genes is: W_5-Y-W_6, with about 25 percent of crossing over in each region.

Gene w_7 is not linked with y.

Genes w_8 and w_9 are two independent duplicate genes.

LITERATURE CITED

ANDERSON, E. G., 1921 The inheritance of salmon silk color in maize. Cornell Univ. Agric. Exp. Sta. Memoir **48**: 535-554.

EMERSON, R. A., 1912 The inheritance of certain forms of chlorophyll reduction in corn leaves. Nebraska Agric. Exp. Sta. Ann. Rpt. **25**: 89-105.

1916 The calculation of linkage intensities. Amer. Nat. **50**: 411-420.

1921 The genetic relations of plant colors in maize. Cornell Univ. Agric. Exp. Sta. Memoir **39**: 1-156.

GERNERT, W. B., 1912 The analysis of characters in corn and their behavior in transmission. Univ. Illinois (thesis). 58 pp. Urbana, Illinois: Published by the author.

HALSTED, B. D., and KELSEY, JAMES A., 1904 Experiments in crossing sweet corn. A new variety: the Voorhees Red. New Jersey Agric. Exp. Sta. Bull. 170, 22 pp.

HUTCHISON, C. B., 1922 Heritable variations in maize. Jour. Amer. Soc. Agron. **14**: 73-78.

KEMPTON, J. H., 1917 A correlation between endosperm color and albinism in maize. Jour. Washington Acad. Sci. **7**: 146-149.

LINDSTROM, E. W., 1918 Chlorophyll inheritance in maize. Cornell Univ. Agric. Exp. Sta. Memoir 13. 68 pp.

1920 Chlorophyll factors of maize. Jour. Heredity **11**: 269-277.

1921 Concerning the inheritance of green and yellow pigments in maize seedlings. Genetics **6**: 91-110.

MILES, F. C., 1915 A genetic and cytological study of certain types of albinism in maize. Jour. Genetics **4**: 193-214.

NILSSON-EHLE, H., 1922 Über freie Kombination und Koppelung verschiedener Chlorophyll-erbeinheiten bei Gerste. Hereditas **3**: 191-199.

RANDOLPH, L. F., 1922 Cytology of chlorophyll types of maize. Bot. Gaz. **73**: 337-375.

TROW, A. H., 1916 On "albinism" in *Senecio vulgaris* L. Jour. Genetics **6**: 65-74.

APPENDIX—Tables 28 to 38

TABLE 28

F_2 data from the cross between stocks 3 and 1.

F_1 PEDIGREE NUMBERS	*W*	*w*	TOTAL	CALCULATED *w*	DIFFERENCE
	9 : 7 ratios				
812– 2	187	143	330	144.6	1.6 ± 6.08
– 5	120	105	225	98.4	6.6 ± 5.02
– 8	153	118	271	118.3	.3 ± 5.51
–10	189	124	313	137.0	13.0 ± 5.92
Total	649	490	1139	498.3	8.3 ±11.3
	3 : 1 ratios				
812– 4	282	78	360	90.0	12.0 ± 5.54
– 7	234	82	316	79.0	3.0 ± 5.19
–13	241	66	307	76.75	10.75± 5.12
–14	255	89	344	86.0	3.0 ± 5.42
Total	1012	315	1327	331.75	16.75±10.6
812– 3	Homozygous for green				

TABLE 29

F_2 data from the cross between stocks 6 and 1.

F_1 PEDIGREE NUMBERS	*W*	*w*	TOTAL	CALCULATED *w*	DIFFERENCE
	9 : 7 ratio				
815–7	129	94	223	98.0	4.0 ±5.0
	15 : 1 ratio				
815–6	215	16	231	14.2	1.8 ±2.48
	3 : 1 ratios				
815–2	90	20	110	27.5	7.5 ±3.06
–3	192	40	232	58.0	18.0 ±4.45
–4	88	27	115	28.75	1.75±3.13
–8	84	23	107	26.75	3.75±3.2
815– 5, – 9, –10	Homozygous for green				

TABLE 30

F_2 data of a cross $W_2 W_2 S_h S_h \times W_2 w_2 s_h s_h$.

PEDIGREE NUMBERS		NUMBER OF SEEDS PLANTED			NUMBER OF SEEDLINGS			
					Sh		*sh*	
F_3	Parents	*Sh*	*sh*	Total	*W*	*w*	*W*	*w*
816– 2	345– 7×334–1	191	48	239	140	43	35	6
– 4		217	79	296	160	36	57	10
– 6		226	76	302	160	47	47	23
– 8		163	56	219	112	39	27	16
– 9		157	49	206	94	33	30	13
816– 1	} green							
– 5								
– 7								
817– 1	345–17×334–3	97	25	122	61	23	19	3
– 3		130	41	171	95	28	30	7
– 4		131	45	176	78	34	22	14
– 6		159	55	214	112	39	41	11
– 9		159	55	214	121	34	29	18
817– 2	} green							
– 5								
– 8								
–10								
–11								
–12								
819– 4	347– 9×334–3	231	79	310	159	70	48	16
– 6		214	84	298	162	47	35	10
– 7		79	23	102	57	12	15	6
–10		231	67	298	165	52	27	13
–11		192	77	269	146	45	49	16
819– 1	} green							
– 2								
– 8								
– 9								
–12								
–13								
–14								
Totals		2577	859	3436	1822	582	511	182
					2404		693	

TABLE 31

F_2 data of a cross $R\ l_g\ d\ W_3\ W_3 \times r\ L_g\ D\ W_3\ w_3$.

PEDIGREE NUMBERS	*R*								*r*							
	D				*d*				*D*				*d*			
	L_g		l_g		L_g		l_g		L_g		l_g		L_g		l_g	
	W	*w*	*W*	*w*	*W*	*w*	*W*	*w*	*W*	*w*	*W*	*w*	*W*	*w*	*W*	*w*
15– 2	177	48							40	16						
– 3	238	60							76	21						
– 4	127	65							48	8						
– 5	113	24	36	13	27	7	9	8	29	13	18	4	8	5	3	2
– 7	103	26	34	11	31	6	11	3	26	5	13	4	16	2	4	2
–18	126	51	49	21					36	16	17	4				
Total for *R r*	884	274	119	45	58	13	20	11	255	79	48	12	24	7	7	4
Total for *D d*	216	50	70	24	58	13	20	11	55	18	21	8	24	7	7	4
Total for $L_g\ l_g$	342	101	119	45					91	34	38	12				

TABLE 32

F_2 data from a cross $r\ P_r\ W_3\ w_3 \times R\ p_r\ W_3\ W_3$.

PEDIGREE NUMBERS	*R*				*r*		TOTAL
	P_r		p_r				
	W	*w*	*W*	*w*	*W*	*w*	
13– 3	133	37			46	21	237
– 4	145	45			40	18	248
– 5	160	64			59	20	303
–10	116	35	32	13	49	18	203
–16	91	29	35	11	53	25	244
Total for *R r*	645	210	67	24	247	102	1295
Total for $P_r\ p_r$	207	64	67	24			362

TABLE 33

F_2 data from the cross between stocks 2 and 4.

F_1 PEDIGREE NUMBERS	S_{II}		S_{II}						NOT CLASSIFIED		TOTAL		CALCULATED	DIFFERENCE
	W	w	Y		Y_p		$y+yp$							
			W	w	W	w	W	w	W	w	W	w	w	
	9 : 7 ratios													
332– 2	42	25	90	80	32	14	11	4	34	21	209	144	154.5	10.5 ±6.29
– 4	20	22	50	32	14	9	5	4	30	26	89	67	68.25	1.25±4.18
–12	13	9	60	48	14	13	6	4	24	27	93	74	73.0	1.0 ±4.32
Total.....	75	56	200	160	60	36	22	12	88	74	391	285	295.75	10.75±8.7
	3 : 1 ratios													
332–1	54	17	146	34	35	12	12	3	47	11	294	77	92.75	15.75±5.63
–7	42	16	111	35	30	11	9	2	45	18	237	82	79.75	2.25±5.22
–8	45	13	94	37	24	10	9	2	39	10	211	72	70.75	1.25±4.91
Total.....	141	46	351	106	89	33	30	7	131	39	742	231	243.25	12.25±9.11
332–5	Homozygous for green													
–6														
–9														

TABLE 34

F_2 progenies from the cross between stocks 2 and 4.

PEDIGREE NUMBERS		W	w	TOTAL	CALCULATED w	DIFFERENCE
F_3	F_4					
I. F_2 progenies from ears segregating in 9 : 7 ratios						
	9 : 7 ratios					
794–3	332– 4	69	50	119	52.1	2.1± 3.65
–5		96	92	188	82.2	9.8± 4.59
–8		16	19	35	15.4	3.6± 1.98
796–1	332–12	157	101	258	112.7	11.7± 5.37
–3		30	24	54	23.7	.3± 2.46
–5		197	126	323	141.3	14.3± 6.01
Total.....		565	412	977	427.4	15.4±10.46
	3 : 1 ratios					
794–2	332– 4	176	71	247	61.8	9.2± 4.59
–4		147	43	190	47.5	4.5± 4.03
–6		207	80	287	71.7	8.3± 4.95
–7		66	12	78	19.5	7.5± 2.58
Total.....		596	206	802	200.5	5.5± 8.27
	Homozygous for green					
795–10	332– 2					
796– 4	332–12					
II. F_3 progenies from ears segregating in 3 : 1 ratios						
	3 : 1 ratios					
797–4	332– 7	178	66	244	61.0	5.0± 4.56
–5		140	40	180	45.0	5.0± 3.92
–7		69	17	86	21.5	4.5± 2.71
Total.....		387	123	510	127.5	4.5± 6.6
	Homozygous for green					
797–1						
–8						
332–7						

TABLE 35

F_2 data from the cross between stocks 6 and 2.

F_3 PEDIGREE NUMBERS	*W*	*w*	TOTAL	CALCULATED *w*	DIFFERENCE
	63 : 1 ratios				
814– 1	83	2	85	1.33	.67± .77
– 9	113	3	116	1.81	1.19± .90
Total.....	196	5	201	3.14	1.86±1.19
	15 : 1 ratios				
814–11	82	6	88	5.5	.5 ±1.53
–12	98	5	103	6.44	1.44±1.66
Total.....	180	11	191	11.94	.94±2.26
	3 : 1 ratios				
814– 8	125	28	153	38.25	10.25±3.61
–14	92	27	119	29.75	2.75±3.19
Total.....	217	55	272	68.00	13.00±4.82
814–13 –15	Homozygous for green				

TABLE 36

F_2 data from a cross between stocks 8 and 3.

F_1 PEDIGREE NUMBERS	*W*	*w*	TOTAL	CALCULATED *w*	DIFFERENCE
	9 : 7 ratios				
800– 4	194	110	304	133.0	23.0 ±5.83
–11	141	87	228	99.75	12.75±5.05
–12	152	97	249	109.0	12.0 ±5.28
	45 : 19 ratio				
800– 5	339	155	494	146.6	8.4 ±6.85
	15 : 1 ratio				
800– 3	183	11	194	12.1	1.1 ±2.27
	3 : 1 ratios				
800– 2	233	70	303	75.8	5.8 ±5.08
– 6	286	59	345	86.2	27.2 ±5.42
– 7	159	44	203	50.7	6.7 ±4.16
–13	274	65	339	84.8	19.8 ±5.38
800– 1	Homozygous for green				
– 8					
– 9					
–10					
–15					
–17					

TABLE 37

Showing the segregation in stock 11.

PEDIGREE NUMBERS		SEEDLINGS	
Offspring	Parents	*W*	*w*
82–10	A1975– 2	94	14
337– 2	82–10	60	16
– 7		38	5
784– 3	337– 7	9	1
–10		7	3
–11		24	1
–12		29	3
–13		62	3
–16		8	3

TABLE 38

F_2 data from the cross between stocks 11 and 3.

F_2 PEDIGREE NUMBERS	*Y*		*y*		TOTAL			CALCULATED *w*	DIFFERENCE
	W	*w*	*W*	*w*	*W*	*w*	Total		
	3 : 1 ratios. Linkage between *y* and *w*								
803– 7	86	23	13	18	99	41	140	35	6.00±3.46
– 9	164	14	22	36	186	50	236	59	9.00±4.49
Total.....	250	37	35	54	285	91	376	94	3.00±5.66
	3 : 1 ratios; no linkage between *y* and *w*								
802– 1	36	15	11	4	47	19	66	16.50	2.5 ±2.37
803– 3	43	7	12	3	55	10	65	16.25	6.25±2.35
– 4	10	3	3	1	13	4	17	4.25	.25±1.20
– 5	24	9	10	2	34	11	45	11.25	.25±1.96
–11	96	23	34	7	130	30	160	40.00	10.0 ±3.69
–12	71	12	19	5	90	17	107	26.75	9.75±3.02
–16	48	22	22	3	70	25	95	23.75	1.25±2.85
Total.....	328	91	111	25	439	116	555	138.75	22.75±6.88
	9 : 1 ratios								
801– 3	125	3	13	12	138	15	153	9.2 : 1	(Observed ratio)
802– 2	125	5	28	12	153	17	170	9.0 : 1	(Observed ratio)
803–13	99	4	19	9	118	13	131	9.07 : 1	(Observed ratio)
Total.....	349	12	60	33	409	45	454		
	9 : 7 or 2.08 : 1 ratios								
803–10	47	20	8	15	55	35	90	9 : 7	6.4 ±3.17
								2.08 : 1	3.8 ±3.06
–17	51	31	15	7	66	38	104	9 : 7	7.5 ±3.41
								2.08 : 1	4.2 ±3.3
–18	91	38	14	22	105	60	165	9 : 7	12.2 ±4.3
								2.08 : 1	6.4 ±4.18
Total.....	189	89	37	44	226	133	359		
	28.59 : 1 ratio								
803–15	78	[illegible]	6	1	84	1	85	2.86	1.86±1.1
803– 6	Homozygous for green								
– 8									
–14									

THE INHERITANCE OF SICKLE-CELL ANAEMIA IN MAN[1]

W. H. TALIAFERRO AND J. G. HUCK

The Johns Hopkins University, Baltimore, Maryland

Received October 29, 1923

In a recent paper, one of the authors (HUCK 1923) has given an account of a comparatively rare disease, so far described only in negroes and mulattoes, which is known as sickle-cell anaemia. The two genealogical charts which his data contain indicate so clearly that the disease is definitely inherited that they seem well worth an analysis.

Only a few salient features of the disease need to be noted here, since a full account of the history, symptomatology, treatment, etc., may be found in the paper mentioned above. The peculiar feature of the disease is the occurrence of crescentic or sickle-shaped erythrocytes when the blood is observed *in vitro*. This phenomenon is due to some alteration (probably taking place in the bone marrow) in the blood cells, and not in the serum, because, when normal red blood cells are suspended in serum from a patient suffering from sickle-cell anaemia, they are not changed, but when red blood cells from such a patient are suspended in normal serum they become typically sickle-shaped. Stained smears or freshly made wet preparations generally reveal only a few sickle cells, but wet preparations which are allowed to stand for 24 hours show from 25 to 100 percent sickle cells according to the severity of the disease. Symptoms of the disease may be absent, mild or severe. Generally, only those patients with severe symptoms, such as varying degrees of weakness and anaemia, leg ulcers and muscular pains or stiffness, seek medical advice, but examination of members of their families often reveal the milder cases.

The chart in figure 1 shows the extent of the disease in the family of John T. of Virginia. Here, the father, John T., with sickle cells, and his wife, Annie T., normal, had seven children, of whom five exhibited sickle cells, one was normal, and one died of pneumonia before the study began. Three of the children with sickle cells married normal persons, and, of their children in each case, part were normal and part possessed sickle cells.

[1] From the Department of Medical Zoölogy of the School of Hygiene and Public Health, JOHNS HOPKINS UNIVERSITY, and the Biological Division of the Medical Clinic, JOHNS HOPKINS UNIVERSITY and HOSPITAL. The present note was written by W. H. TALIAFERRO, but is based on the original data of J. G. HUCK.

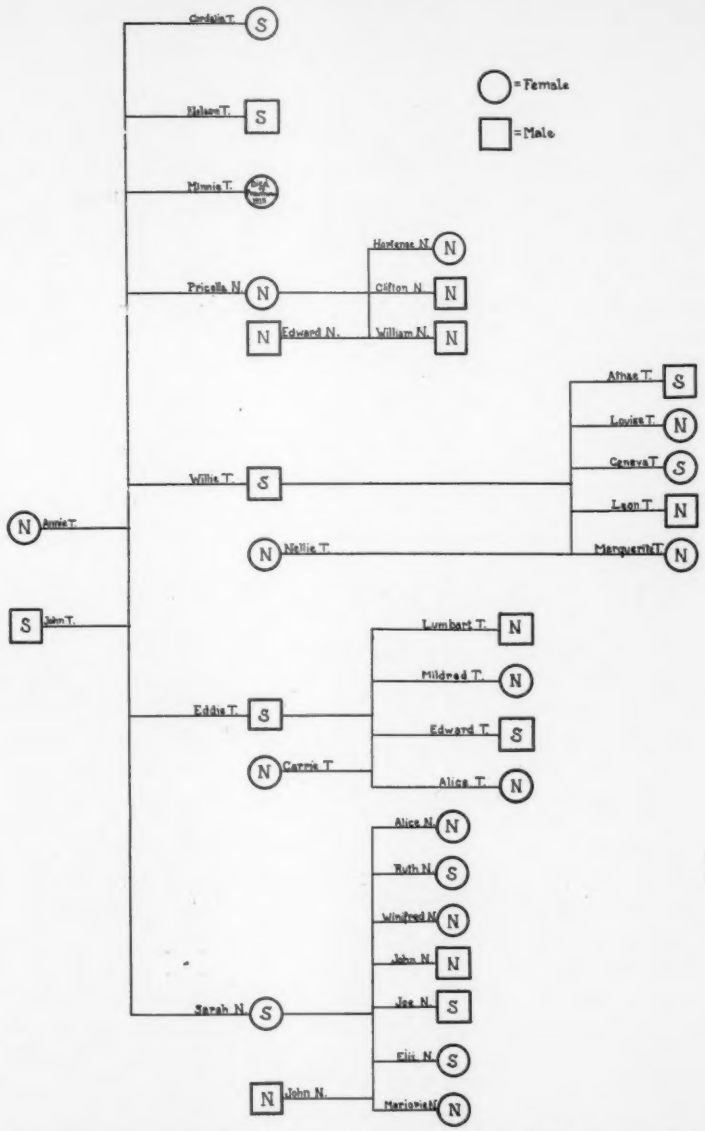
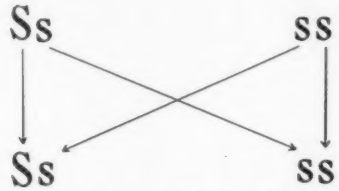


FIGURE 1.—Chart showing the inheritance of sickle cells in the family of John T of Virginia. *N*, normal, and *S*, sickle cells.

The children of the one normal child who also married a normal person were all normal. In analyzing this chart it seems best to give what we believe to be the correct explanation of the inheritance of sickle cells and follow this with a short discussion of the other possibilities which have been eliminated.

Careful examination of the chart in figure 1 reveals the fact that the character for sickle cells behaves as a single Mendelian character, which is not sex-linked, and which is dominant over the normal condition. Furthermore, John T. seems to be heterozygous for the sickle-cell condition and his wife homozygous for the normal condition. The following diagram shows the results which would be expected under such conditions, where *S* stands for the sickle-cell character and *s* for the normal character.



The fact that of the six F_1 progeny of John T. and Annie T., which were tested, only one was normal, seems a rather poor approximation to the expected 1 : 1 ratio. If, however, John T. is heterozygous, then all of his abnormal children must be heterozygous, and we are justified in averaging the results obtained from the marriage of John T. and Annie T. with the progeny resulting from the marriages of their abnormal children with normal mates. In this way we have four crosses of presumably heterozygous abnormal persons with homozygous normal persons. Resulting from these four crosses, there are 23 children as follows: John T.×Annie T., 5 abnormal, 1 normal and 1 untested; John N.×Sarah N., 3 abnormal and 4 normal; Eddie T.×Carrie T., 1 abnormal and 3 normal; Willie T.× Nellie T., 2 abnormal and 3 normal. In the total of 23 children, there are 11 abnormal, 11 normal and 1 untested, which gives, among the tested children, an exact 1 : 1 ratio.

Not only are the results charted in figure 1 in accord with the assumption that sickle-cell anaemia behaves as a single Mendelian character which is dominant over the normal condition and is not sex-linked, and that John T. is heterozygous for the abnormal condition, but we have found them to be incompatible with other possible assumptions. It is unnecessary to present all of these, as some of them are obviously unsuitable, but a few should be noted.

1. In the original cross between John T. and Annie T., the former may have been homozygous for the abnormal condition and the one normal child may have been illegitimate. If this be true, however, the children would all be heterozygous, just as when John T. is assumed to be heterozygous, and hence the main conclusion that sickle-cell anaemia behaves as a single dominant Mendelian character would be unaffected.

2. It is obviously impossible to consider the character of sickle cells a sex-linked dominant, because then the F_1 generation would have consisted of only abnormal daughters and normal sons. If, on the other hand, the character were a sex-linked recessive,[2] and Annie T. were heterozygous for

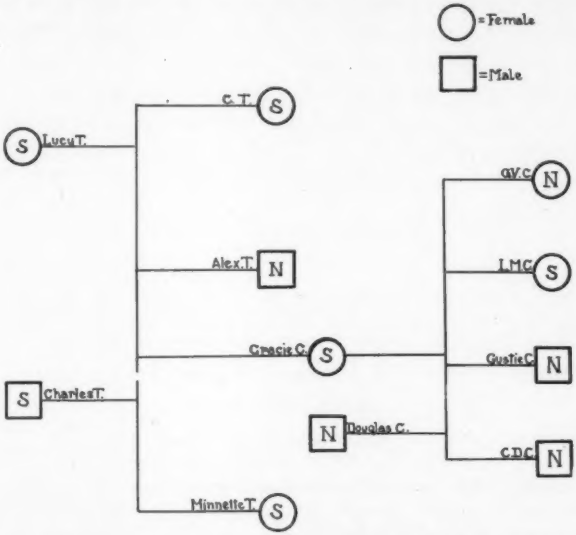


FIGURE 2.—Chart showing the inheritance of sickle cells in the family of Charles T. of Maryland. *N*, normal, and *S*, sickle cells.

the sickle-cell condition, we may assume that the expected ratio of an equal number of normal and abnormal sons and daughters was not obtained because of the smallness of the numbers involved. That this explanation is based on a false assumption, however, is shown by the fact that the F_1 abnormal daughters (who must be homozygous) when mated with

[2] This analysis of sex-linked inheritance is based on the assumption that in man the male possesses an *X Y* and the female possesses an *XX* chromosomal complex, as is indicated by the recent work of PAINTER (1923). That this is a correct assumption is also indicated by the behavior of the known sex-linked characters in man.

normal men should have had only normal daughters and abnormal sons, an expectation which is not borne out by the facts.

3. It may be that the character for sickle cells is a non-sex-linked recessive and that Annie T. is heterozygous (John T. being necessarily homozygous), in which case the progeny should consist of an equal number of normal and abnormal children. In this case, however, the only way to explain the results obtained in the F_2 generation would be to assume that each abnormal child married a person heterozygous for the sickle-cell condition. This assumption seems beside the point when we can fit the facts in the case so much more readily as described in our first analysis.

The chart shown in figure 2, which is taken from the data of GUTHRIE and HUCK (1923), contains too few individuals to warrant a detailed analysis. The results are, however, easily explained by assuming, as was done in the first case, that the character for sickle cells is a single Mendelian dominant which is not sex-linked and that both Charles T.[3] and Lucy T. are heterozygous for sickle cells. It does, therefore, add further evidence for the correctness of the conclusions reached in the analysis of the first chart.

SUMMARY

Sickle-cell anaemia in man is an inherited condition and behaves as a single Mendelian character which is dominant over the normal condition and which is not sex-linked.

LITERATURE CITED

GUTHRIE, C. G., and HUCK, J. G., 1923 On the existence of more than four iso-agglutinin groups in human blood. (Part I). Bull. Johns Hopkins Hosp. **34**: 37-48.

HUCK, J. G., 1923 Sickle-cell anaemia. Bull. Johns Hopkins Hosp. **34**: 335-344.

PAINTER, T. S., 1923 Studies in mammalian spermatogenesis. II. The spermatogenesis of man. Jour. Exp. Zoöl. **37**: 291-336.

[3] Although the surnames of the original members of the families shown in the charts in both figures 1 and 2 begin with T., their names are different, they come from different states and are probably not even remotely related.

JOURNAL *of* GENETICS

Edited by

W. BATESON AND R. C. PUNNETT

Founded in 1910, the Journal of Genetics is the only British periodical devoted to the publication of original research in Heredity and Variation. Up to the end of 1922 twelve volumes have been completed. The illustrations form a feature of the series, for, in addition to numerous text figures and diagrams, the twelve volumes contain 262 plates, of which 54 are in colours.

Many of the papers published deal with animals and plants of high economic value, and are therefore of interest to those concerned with agriculture and horticulture.

A full index to Vols. I-XII was issued with the last part of Vol. XII.

The Journal of Genetics is published in parts, of which three form a volume. Approximately one volume is issued annually. The subscription price for a volume is £2.2.0 net; the price of the separate parts being 15 shillings net each. The parts are sent post free to subscribers as issued.

Subscriptions, payable in advance, should be sent to Mr. C. F. Clay, Cambridge University Press, Fetter Lane, London.

The Cambridge University Press has appointed THE UNIVERSITY OF CHICAGO PRESS agent for the sale of the Journal of Genetics in the United States of America, and has authorized the following prices:—Annual subscription $10.00 net; single copies $3.50 net each.

Inquiry as to back numbers should be made of Mr. C. F. Clay. Separate parts and volumes are still available in some cases.

Brooklyn Botanic Garden Memoirs

Volume II

The Vegetation of Long Island

Part I

The Vegetation of Montauk

A Study of Grassland and Forest

By NORMAN TAYLOR

Price, $1.00. Remittance should accompany all orders. Published June 11, 1923. Not offered in exchange.
108 pages, 30 text figures

Address
The Secretary, BROOKLYN BOTANIC GARDEN, *Brooklyn, N. Y., U. S. A.*

Ecology

Devoted to All Forms of Life in Relation to Environment

Established 1920 Quarterly

Official Publication of the Ecological Society of America

Subscription, $4 a year. Back volumes I-III, $3.50 each, post free
Foreign postage: To Canada 10 cents; to other countries, 20 cents.
Single numbers $1.15 post free.

Published by BROOKLYN BOTANIC GARDEN, *Brooklyn, N. Y., U. S. A.*

Bibliographic Service in BOOK FORM, Volume 1

1922. Bibliographic Service in book form with authors' and analytical subject indices, covering two and a half years of the Bibliographic Card Service, June 1, 1917, to December 30, 1919, cards nos. 1 to 519 **Price, $5.00**

To subscribers to the Bibliographic Service, covering this period, 50 per cent discount

Volume II in preparation

THE WISTAR INSTITUTE OF ANATOMY AND BIOLOGY
PHILADELPHIA

INDEX

Prepared by Doctor Allan C. Fraser and Mrs. G. W. Beadle. Page numbers printed in black-faced type refer to headings of articles or of sections. References to names in lists of "Literature cited" are given in italics.

Adzuki Bean
  Absence of certain character combinations in F_2 170
  Absence of sterility 169
  Automatic self-pollination 168
  Color intensifier 174–176
  Color of ripe pods
    Blackish brown 169–173, 176
    Brown 169–174, 176
    3:1 ratio 174
  Color of stems
    Classification 169
    Dark reddish purple 170–172, 176
    Factor for red-purple stem 175
    Green 169, 170, 172–174, 176
    Interaction of two factors 174
    Light reddish purple 169–173, 175, 176
    Linkage with seed coat color 174
    Purpling factor, *P* 174–177
    Variation with age 169
  Correlation of stem color with seed coat color 174, 175
  Crossing over 175–177
  Factor for black spotting, *S* 176
  Factor for blackish brown ripe pods, *B* 176
  Linkages 168–177
    Color intensifier and seed coat factor 176, 177
    Colored stem and black spotted seed coat 174, 175
    P and *S* 176, 177
    Partial linkage 177
  Seed coat color 169–173, 175
    Black 175
    Dark blue 175
    Deep blue spotted on yellow green 175
    Intensely black spotted red coats 169–173, 175, 176
    Less intensely black spotted coats 170–173, 176
    Non-black 175
    Ratio 1:2:1 for spotting 174
    Unspotted red coats 169–174, 176
  Varieties
    Donsu 169, 176, 177
    Kensaki 175
    Kon-adzuki 175
    Kuro-adzuki 175
    Midori-yogore-adzuki 175
    Myako 169, 176, 177
    Yogore-adzuki 175
Aegilops ovata 312
Aleurone in maize 467, 470–472
Alfalfa 208
  Plot tests 194, 195
ALLARD, H. A. 121, *152*
ALLEN, EZRA 2, *26*
ALLEN, RUTH 316, *320*
Almond 390, 391, 458
  Blooming period 390
    Commercial varieties 390
    Susceptibility to frost 390
  Crosses
    Heterozygosity 390, 391
    Ratios 390, 391
  Data
    Numbers of seeds planted 390
    Numbers of sweet and bitter trees 390, 391
    Numbers of trees planted 390
    Ratio of totals 390, 391
  Genetic constitution
    Factors for bitterness 390, 391
    Possible mutation 391
  Varieties
    Commercial varieties 390
    IXL 390
    Ne Plus Ultra 390
    Nonpareil 390
ALTENBURG, E. *300*
ANDERSON, E. G. 466, *475*, 563, 575, 582, *585*
Anthocyanin in maize 475
ANTHONY, R. D. 182, 183, 187, 196, *210*
Apatura 541
Aphids, transmitting disease in potatoes 189
Apple 458
Apples
  Baldwin 460
  Ben Davis 179–186, 190, 195–197, 199, 200, 207, 208, 210, 464
    Correlations of yield—interannual 185, 191, 197–199, 208
    Variation curves 179
    Variation in single individual 179
    Variation in yield 179, 185
    Variation of given character 179
    Yield of fruit 180, 185, 186, 190–192
  Bud mutation 202, 461, 462, 464
  Bud selection 202–205, 209
  Bud variation 183, 202
  Comparison of variation in yield with that of orange 184
  Correction factor for eliminating effect of varietal differences in apples 463
  Correlations
    Between variety and size 461
    Interannual-yields for one clone 184, 185

Apples (continued)
Correlations (continued)
Size on French Crab and Tolman Sweet roots 461
Stock, scion, and year budded, with tree size 461
Yield 197, 198
Dwarf stocks 200, 202, 204
Effect of fertilizers 183
Effect of soil heterogeneity 179, 190, 192
Factors producing variability in yield 186, 190
French Crab stock 200, 201, 204, 459–463
Gravenstein 460
Heterozygous nature 201
Jonathan 182, 184, 196, 197, 200, 207, 208
Larue 460
McIntosh 460
Milding 460
"Naturals" 201, 459
Permanence of performance in a clonal variety 179–211
Relation of trunk circumference to productivity 464
Rolfe 460
Rome 182–184, 187, 190, 195–197, 200, 207, 208, 210
Effect of fertilizers 183
Permanence of performance 187, 188
Top-worked on Ben Davis 182, 183, 187
Scarcity of bud variations 200, 209
Self sterility 200
Spy 460, 461
Stark 460, 461
Tolman Sweet 460, 461, 463
Tree individuality 183, 190
Variability in French Crab stock 201, 208, 461
Variation in stocks 200, 201
Variation in yields of clonal varieties 181, 182, 190
Variation in yields of clones 182–184
Variations in individual trees 183, 184
Wealthy 460
Apricot 458
Arcella
Abnormality due to environmental conditions 489
Appearance of a double organism 478, 492
Atavism 484, 485, 492
Comparison of fission rates in normal and abnormal specimens 482, 492
Correlation between size and abnormality 487, 493
Correlation between size and nuclear material 491
dentata 492
Description of double organism 479
Description of organism 478, 479
discoides 492
Double characteristics 477–493
Double forms physiologically comparable to a single individual 490
Arcella (continued)
Doubleness produced by failure of complete fission 492
Doubling of nuclei in cut pieces 492
Increase in size in cut pieces 492
Mass culture 485, 493
Mechanical influence of parent shell on shape of offspring 491
Method of culture and investigation 479–481, 483
Method of measuring 485–487
Obtaining normal forms from abnormal ones 483
Occurrence of abnormal specimens in nature 489
polypora 477–493
Presence of many nuclei in normal individual 478, 491
Return of abnormal clones to normal condition 481, 483, 492
Selecting for greater abnormality 483, 484, 492
Uneven division of nuclei at time of fission 492
Arctiidae 496
Argynnis
Breeding experiments 538, 539
Distribution 538
Dominant "melanic" type 537, 538, 547
Genotypes 538
Homozygous *valesina* 538
Inheritance 538, 539
paphia 537, 538. 547
paphia var. *valesina* 537, 538, 547
Pedigrees of *paphia* and *valesina* 540
Precocity of males 541
Semi-lethal nature of *valesina* 538
Wing color due to single dominant factor 537
Aristolochia 532
ARISTOTLE 336, 546
ARMSTRONG, S. F. 316, 317, *320*
Arrangement of genes in a linear series 393–457
Asexual propagation in Crepis 228, 232
Athyrium filix-femina 87
Avena
barbata 315
brevis 315
sativa 315

BABCOCK, E. B. 28, *104*, 212, *232*
Backcross
In determining linkage intensities 106
Practical difficulties attending backcross in certain crops 106
BAER, CHARLES *87*
BAILEY, L. H. 315, *321*
Balanced lethals
In Colias 516
In Drosophila 284, 285, 299
In Oenothera 159, 160, 286
BALBIANI, E. G. 477, *493*
BARKER, E. E. 119, 150, *152*
BARRUS, M. F. 189, *210*

BARTLETT, H. H. 161, *167*, 468, *476*
"Basic propositions" for linear arrangement of genes 397–399
BATCHELOR, L. D. 182, 184, 196, *210*
BATESON, W. 102, *104*, 146, *152*, 322, 333, *334*
BAUR, E. 27, *35*, 102, *104*, 537, *550*
BEAN, T. E. 526, 549
Beans 552
Adzuki beans 162–177
Association of size differences with seed coat pattern and pigmentation 552–560
Association of size factors with mottling and extension factors 558
Blending inheritance 558–560
Correlation between bean weight and eye pattern 556
Correlation between bean weight and plant size 556
Correlation between F_1 bean weight and F_2 pattern 556
Correlation between F_2 size and resulting F_3 segregates 557
Cranberry 557
Crossing over between eye factor and size factors 558
Crossing over between pigmentation factors and size factors 558
Cumulative effect of size factors 558–560
Difference in effect of size factors 558, 560
Dot Eye 553
Dot Eye×White, 1228 554–558
Effect of size factors in different linkage groups 558
Extension factor, *T*, for pigmentation 553
"Eyed" bean due to recessive *t* 553
Factors for black, brown and purple color 553
Genetic behavior of crosses 553, 554
Heterosis hypothesis 559, 560
Improved Yellow Eye 553, 554, 556–559
Improved Yellow Eye×Cranberry 557
Improved Yellow Eye×White 1228 554, 556–559
Improved Yellow Eye×White 1333 553, 555, 558
Inheritance of pattern and pigmentation complex 553
Marbling of seed coat 174
Mottling dependent on linked factors *Y* and *Z* 553, 559
Number of size factors 557
Obtaining individual bean weights 553
Pigmentation dependent on factor *P* 553, 554, 559
Procedure in experiment 553
Seed weight in various classes of segregates 554–556
Beets, root form 131
Behavior of size factors in rabbits 559
BEHRE, E. H. 351, *353*
BELLAMY, A. W. 351, *353*
BELLING, J. 214, *232*, 304, *320*
BENEDICT, R. C. 75, 80, 81, 86, 87, *95*
BENTON, F. 542, *550*
BICKFORD, 351
BIFFEN, R. H. 302, 312, 314, 316, *320*
Bilaterality 339, 340
Black leghorns 332
BLAKESLEE, A. F. 86, 89, *95*, 103, *104*, 155, 186, 237, *238*
Blond ring-dove 546
BOEDJIN, K. 233, *238*
BOISSIER, E. 213, *232*
Bombyx mori 322
Allelomorphs in egg color 327, 329
Backcrosses 326, 327
Brown eggs 324, 333
Crosses 324–327
Diagram of crosses 327
Diagram of generations 325
Diagram of genotypes and phenotypes 330, 331
Effect of temperature on voltinism 324, 333
Egg color 322
Genotypes for egg color 329
Mendelian ratio in egg color 326–329
"Mixed" 324, 333
Normal 324
Phenotypes for egg color 324
Voltinism 322, 333
Zygotic constitution 328, 329
BOSHNAKIAN, S. 261, 262, 263, *275*
Boston Fern 75–80, 86–93, 95 (See *Nephrolepis exalta bostoniensis*)
Bouvardia
Bridesmaid 102
Bud variation in 102, 103
Chimeras in 102
Hogarth 102, 103
Interspecific hybridization in 103
leiantha 103
longiflora 103
Not always true from root cuttings 102, 103
BOVERI, TH. 332, 333, *334*
Brachytic culms in maize 470, 475
Brassica chinensis (See Pe-tsai)
Brassica oleracea (See Cabbage)
BREITENBECHER, J. K. 539, 541, *547*
BRIDGES, C. B. 28, *35*, 102, *105*, 277, 281, 289–292, *300*, 315, *320*, 337, *354*, 355, *366*, 394, 395, 397, 401, 419, 421, 422, 432, 445, 450, 451, 452, 453, *456*, *457*
Bronze-wing turtle dove 546
BROWN, A. F. 340, *354*
Brown Leghorn fowl 367–389
Bruchus quadrimaculatus 537, 539
Body colors 539
Elytral colors 539
Sex-controlled characters 539
Somatic variations in female coloration 541
Spotting 539
BUCHANAN, J. W. 351, *353*
Bud mutation
Critique of theory of 179, 184, 202–209
In apples 461, 462, 469

Bud mutation (continued)
In citrus 202, 204, 206, 209, 210
Rarity in varieties of fruit 202
Bud selection 202, 203, 209
Bud sports in Nephrolepis **75**–95
In seed plants 94
Relation to origin of new species 92
Bud variation (See Chimeras)
By chromosome elimination 100, 102
By point mutation 100
Cellular changes involved 102
In Bouvardia 102, 103
In Citrus 104
In *Matthiola annua* 102
In Nectarine 104
In Nicotiana 97–105
"Reverting" branches 103
Study of genetic nature of 103
Bunt on wheat 314
Butterflies 90 (See Pierid butterflies)

Cabbage crossed with radish 131, 150
Cabbage butterflies (See Pieris)
CARPENTER, C. *35*
CASTLE, W. E. *35*, 322, *334*, 452, *456*, 552, 557, 559, *560*
Cattle
Guernsey 186
Holstein-Friesian 186
Milk yields in 186
Centropyxis aculeata 479
CHAPMAN, T. A. 541, 542, *550*
Chiasmatypy 165, 166
CHILD, C. H. **336**, 339, 343, 351, *353*
CHILDS, JOHN LEWIS 87
Chimeras
By chromosome elimination 100, 102
From grafts 103
In Nicotiana
Clonal studies 99, 100
Genetical tests 97, 98
Periclinal chimeras in *N. Tabacum* **97**–105
Natural chimeras in cultivated forms 104
Rearrangement of tissues in 103
Relative stability of periclinal chimeras 104
Seed test not always sufficient 103
Solanum-Lycopersicum chimeras 103
Chromosomal complex in man 599
Chromosome aberrations 89, 90, 94
In Datura 89
In Drosophila 89
Chromosome behavior 337
Chromosome elimination 100, 102
Chromosome hypothesis 145
Applicable to plants 145
BATESON'S view of 146
Chromosome number
In Crepis 214, 227, 228
In Digitalis 226
In Nephrolepis 94
In *Nicotiana Tabacum* 100
In oats 315
In Oenothera 234, 235
Chromosome number (continued)
In Oporabia 542
In rats 2
In wheat 304, 305, 319
Chromosome pairing in hybrids 223
Chromosome theory of heredity 337
Ciliates 477, 491
Citrus 104, 190, 205, 209 (See Oranges, Lemons)
Bud mutation 202, 204, 206, 207, 209, 210
Difference in tree performance due to soil heterogeneity 179, 190, 192, 193, 202
Difference in tree performance due to stocks 202
Establishment of uniform stocks 202
Heterozygosity 202
Top-working trees 205–207
CLARK, J. A. 317, *321*
CLAUSEN, R. E. 28, 97, *104*, 277, 282, 287, 296–298, *334*
CLAUSEN'S Method 287
CLEGHORN, M. L. *322*, *334*
CLELAND, R. E. 165, *167*, 236, 237, *238*
Clonal varieties
High degree of variation in yield 182, 184
Materials for study 180
Methods of study 180
Permanence of tree performance 179–211
Variation in performance 179, 186, 187, 207
Due to bud mutation 179, 190, 199, 200, 202–207, 209
Due to soil heterogeneity 190–200, 207, 208
Due to variable stocks 179, 190, 191, 197, 199, 200–202, 207, 208, 210
Variation in yield in potatoes 182, 184, 187, 188, 190
Variation within 189
Clone 478
In apple 179–210, **458**–465
In Nicotiana 99, 103
COBB, FRIEDA 161, *167*
COHEN, R. 119, 150, *152*
COLE, L. J. 546, *550*
Colias
Absence of expected yellow individuals 501
Arctic species 531
Balanced lethals 516
Blue-green caterpillars 503, 504, 516
Breeding experiments with *C. christina* 526–528, 547
Breeding experiments with *C. myrmidone* 528–529
christina 496, 526, 547
Classes of female coloration 499, 547
Climate and wing color 528–532, 547
Comparison with Papilio 532–537
Conspectus of matings (facing page)514
Dominant white coloration 506, 547
edusa 496
Epistatic wing colors in male 521, 537
eurytheme 496–498, 500, 506–514, 518, 525, 526, 528, 530, 533, 537, 542–544, 547–549

Colias (continued)
eurytheme eriphyle 529
eurytheme var. *alba* 533
eurytheme×*C. philodoce* 543
Genetic constitutions 537, 547
Grass-green caterpillars 505, 516
Gynandromorph 525, 543
Heterozygosity of wild white females 506, 548
Homozygous white females 500, 528, 548
Homozygotes for white 502, 503
Homozygous white male 500
hyale 496
Hybridization 543–549
Inbreeding homozygotes 503, 504
Inbreeding white-bearing stocks 501
Infertility due to inbreeding 505
Inheritance of female whiteness 505
Inheritance of male color pattern 499
Inheritance of male yellowness 499
Interaction of factor pairs 527
Interbreeding heterozygotes 500
interior 496, 528, 531
Larval blood-color 503–505, 516
Lethal factor associated with *w* 514–519, 548, 549
Mathematical computation of proportion of white 522–525
Mathematical computation of stability of white 521, 522
"Mimics" 532–535
myrmidone 496, 528–531, 547
myrmidone var. *alba* 528, 531, 547
nastes 508
Natural occurrence of white males 532
Occurrence of white females in spring brood 529, 530
Olive-green caterpillars 505, 516
palaeno 531
pelidne 496, 526, 531
philodice 496, 497, 499–502, 506–515, 520, 525, 526, 528–531, 533, 534, 538, 542–544, 547–549
philodice var. *pallidice* 533
Polymorphic females 533
Precocity of the male 541–544, 547
Proportions of white in general population 520–526, 547
Ratio 7:9 519, 520
Recessive normal yellow coloration, *w* 506, 547
Red forms 529, 549
Regular ratios 505–513
Results of previous investigations 419, 420
scudderi 496, 526, 531
Sex ratios 543, 549
Stability of white variety in general population 520–526, 547
Subarctic species 531
Tables of crosses 509–513
Trimorphic females 547
Types of mating 505–520, 547, 548

Colias (continued)
Unexpected ratios 501, 502, 504, 508, 514–517, 549
Univoltine species 526
Viability 544, 550
Wing pattern 497
"Collective action of genes" 337
COLLINS, J. L. **212**, 214, *232*
Compatibility in species crosses 212
CONKLIN, E. G. 323, 332, 333, *334*, 339, *353*, 366
COOLIDGE, 366
Corn
(See Maize)
Ease of getting backcrosses 106
Plot tests 194, 195
CORRENS, C. *334*
Corymorpha
Adventitious axes 346, 350
Description of 344–346
Factors determining axial relations in cut pieces 347
Origin of single and biaxial forms 345
palma 344
Radial symmetry 348
Cow-pea weevil 539 (See Bruchus)
CRAIG, R. A. 85
CRAIG, W. T. 311, 312, *321*
CRAMER, P. J. S. 103, *104*
Crayfish 338
Crepis
Asexual propagation 228, 232
biennis **212**, 221, 223–232
Cell size 231
Chromosomes 212, 223, 224, 226
Crossed with *C. setosa* 221–228
Description of 213, 214
Octoploid species 223, 226, 231
Variation in leaf type 224
capillaris **212**–223, 226, 228, 231, 232
Crossed with *C. setosa* 214–221
Description of 213
Haploid number of chromosomes 212
Chromosome studies 214
Effect of hybridization on chromosome number 228
Methods of crossing 214
Methods of germination of seeds 214
Sections of the genus 213, 214
Barkhausia 213, 214
Eucrepis 213
Gatyona 213
setosa 212, 214–232
Description of 214
Haploid number of chromosomes 212
setosa×*C. biennis* 221–228, 231, 232
Backcrosses 227–228
Chromosome numbers 227–228
Leaf types 229
To *biennis* 227–231
To *setosa* 228, 229
Change from biennial to annual habit 231
Dominance in F_1 232
F_1 hybrids 221–227, 231

Crepis (continued),
setosa×*C. biennis* (continued)
F_2 plants 227, 230
Selfed seed on F_1 plants 232
Setosa×*C. capillaris* 214–221, 228, 231, 232
Backcrosses of 217–221
Chromosomes of F_1 216–221, 226
Chromosomes in resulting plants 217–220, 222, 231
Dominance in F_1 231–232
Irregular cell divisions in 217, 231
Ovules in F_1 217
Pollen of F_1 216, 217
With *C. setosa* 218, 219, 220, 222, 231
tectorum 212
Critique of the theory of bud mutation 179–211
Crossing over
As explained by "linear theory" 393, 400, 401–403, 411, 412
Calculating crossover percent from F_2 results 106
Conditions affecting 452
Crossing over with interference 423–451, 455
Crossing over with no interference 403–418, 421, 423, 425, 454
Duplicate factors, one linked with a third factor 108–110 114,
In Adzuki beans 175–177
In Drosophila 355
In Oenothera
Absence of cytological evidence 154, 165, 166
An "intrazygous" phenomenon 166
Must occur within chromosome pairs 166, 167
Mathematical expression of 404, 416, 421, 423, 425–441, 455
"Crossover ratio" 395
Crossover unit 440, 452, 453
CUÉNOT, L. 545, *550*
CUMMINGS, M. B. 204, 209, *210*
Curly dwarf disease in potatoes 189
Cyclopia in fishes 351
Cynthia 332
Cytoplasmic differentiation in egg 333
Cytoplasmic inheritance 337, 352

"Damping off" in *Raphanus Raphanistrum* 136
DARWIN, C. *35* 595
Datura 237
Chromosome abberations in 89
gigas form 89
Davalliae (fern tribe) 83
DAVENPORT, C. B. 332, *334*, 367, *389*, 498
DAVIS, B. M. 156, 157, 162, 165, *167*
DAVIS, M. B. 203, 209, *210*
DEMEREC, M. 561
DEMOLL, R. 541, *550*
Dennstaedtia cicutarioides 83
DETLEFSEN, J. A. 355, *366*, 452, 453, *456*
DEXTER, J. S. 29, *35*, 300
Didynium 477
nasutum 490

DIGBY, L. 215, *232*
Digitalis
lutea 226
lutea×*D. purpurea* 226
purpurea 226
Dilute sun-red plants in maize 467, 468
Dimorphism in female 496
Dimorphism in male 496
Dimorphism in Oenothera 234
Disease resistance in oats 315
Domestic fowl (See Poultry)
Annual egg record influenced by periods of laying 39
Coefficient of variation in annual egg production 181, 186
Correlations
Between egg laying activities at different periods 37, 46
Between egg records of individual months first and second years 38
Between 1st and 2nd years' production 38
Between times of beginning and cessation of laying in first and second years 37–74
Between times of beginning and cessation of laying, 2nd year 37, 46, 52–56, 63, 67, 68, 72
Between times of beginning of laying and cessation, first year 37, 46, 50–53, 67, 68, 71
Between times of beginning of laying, 1st year and cessation of laying, 2nd year 37, 41, 46, 60–63, 67, 74
Between times of beginning of laying in 1st and 2nd years 37, 39, 46, 48–50, 67, 70
Between times of cessation of laying, 1st year, and beginning of laying, 2nd year 37, 46, 55–60, 63, 67, 73
Influence of heterogeneity on correlations 63–65
Influence of maturity 62, 63
Curves for frequency distributions in times of egg laying 42, 44
Curves for regression of times of egg laying 47, 50, 51, 53, 54, 56, 59
Cycles of laying 62, 63
Egg production in 37–74
Fecundity influenced by rate of growth 38
Heavy laying and conditions influencing 38, 39
Methods of studying periods of egg laying 40
Regression with respect to times of beginning and cessation of laying 47, 50, 51, 53, 54, 56, 59, 61, 67
Relation between precocity and persistence in laying 67
Statistical constants based on time of beginning of egg laying 37, 41–44
Statistical constants based upon time of cessation 37, 41, 44, 45, 46
Time of beginning of laying 41–44, 66
Time of cessation of laying 41

Dominance of size factors in Raphanus 116–153
Dominant genes—in relation to hybrid vigor 117, 151
Double crossing over 401, 403, 404
In Drosophila 24, 31, 291, 293, 356
Double organisms 477, 478
Double worked stocks in fruit propagation 460
Doves
Breeding records 545, 546
Possible precocity of the male 545–547
Sex ratios 545
DRIESCH, H. 332, *334*, 337, 351
Drosophila 233, 236
"IIple" stock 286–288
"IIIple" stock 291
"Xple" stock 287, 290
Accelerated development of germ cells due to X-ray treatment 364
Age, effect on crossing over 355, 364
Apparent cinnabar^2 mutants 276, 285, 299
Apparent vestigial mutants 276, 285, 299
Apterous 278
Arc 420
Balanced lethal factors 276–300
Balloon 278, 449
Bar 395–398, 419, 422, 447, 449, 450
Beaded 278, 284, 285, 299
Bifid 395–397, 399, 422, 450
Black 284, 286, 293, 294, 296–298, 397, 420, 422, 447, 449, 450
Blistered 278
C_{II-III} 289
C_{III-II} 289
Cinnabar 297, 298
Cinnabar^2 271, 277, 285, 297, 299
Cleft 449
Club 278, 395–399, 422, 450
Crossing over in sex chromosome 355
Crossover classes 356
Crossover factor C_{CL} 288
Crossover factor C_{CR} 288
Crossover inhibitors in chromosome II 277
Crossover ratios for chromosome I 395, 396, 419
Crossover ratios for chromosome II 419, 420, 422
Crossover ratios for chromosome III 420
Crossover values—evidence of effect of X-rays 356, 366
Crossover values obtained in X-ray experiment 357–360, 362–365
Culture methods in X-ray experiment 356, 357
Curly wing 276–300
Backcrossing to "IIple" stock 286, 287, 293, 296
Backcrossing to "IIIple" stock 291, 292
Backcrossing to "Xple" stock 290, 291
Balanced lethal nature of stock 284, 285, 299
Crossing over 285
Crossing over between star and curly 289
Crossover factor C_{CL} 288, 289, 297, 299
Crossover factor C_{CR} 288, 289, 299
Drosophila (continued)
Curly wing (continued)
Crossover factors associated with curly 286–288, 295
Crossover percents for backcross at 30°C 295
Curly wing located in second linkage group 276, 283, 286, 299
Description 278, 279
Dominance of character 277, 280, 299
Double crossing over 291, 293, 294
Effect of the associated crossover genes on chromosome I 289–291
Effect of associated crossover genes on chromosome III 291
Effect of higher temperature on crossing over 293, 294, 296
Evaluation of curly 298, 299
Genetic constitution 300
Heterozygosity 280–284
Induced crossing over 288
Lethal in homozygous condition 276, 284, 299
Linkage tests 283
Locus of gene for curly 296, 297, 299
Occasional homozygous survivors 281, 284
Occurrence of twin hybrids 276, 282
Probable origin of curly mutation 295
Selecting for curly 278
Source 277
Triple crossing over 291, 293, 294
Venation figures 279
Viability 277, 287, 298
Curved 284, 286, 288, 289, 293, 294, 397, 419, 420, 422, 447, 449, 450
Cut 278, 283, 290
Dachs 397, 420, 422, 447, 450
Dichaete 397, 420, 447, 449
Differential viability 356, 365
Dosage of X-ray 357, 359, 366
Double-crossing over 31, 356, 357, 365
Dumpy 284, 286, 297, 298
Duration of X-ray effect 363, 366
Echinus 283, 290
Effect of age of mother on crossing over 293
Effect of temperature on crossing over 355
Effect of X-rays on crossing over 355, 357, 359, 363
Effect of X-rays on linkage 355-366
Effect of X-rays on non-disjunction of sex chromosome 355
Eosin eyed 356-366, 449
Evidence for effect of X-rays 356, 357, 364, 366
Fatal injury due to X-ray treatment 363
First chromosome 411, 419, 432
Forked 283, 290, 419, 447, 449
funebris 542
Precocity of female 542
Fused 419, 447
Garnet 283, 290, 419
Genes of chromosome I 396
Genes of chromosome II 397, 399

Drosophila (continued)
Genetic constitutions of flies used in X-ray experiment 357, 359
Hairy 283, 291
Inbreeding in 117, 145
Increase of crossing over due to high temperature 293
Inheritance of decreased crossing over due to X-ray treatment 364, 366
Jaunty 278
Lack of crossing over in X chromosome 399
Lethal factor in larval stages 332
Long winged 356
Loss of chromosomes 89
melanogaster 3, **27**, 36, 276, 298, 299, 393, 420, 449, 542
Abnormal abdomen 29
Beaded 29
Cinnabar 31, 33
Cross of heterozygous normal and eyeless
Excess of normals in controls 3, 4
"High" normal lines 1, 4, 11-26
"Low" normal lines 1, 4, 5-11, 16, 20, 22-24, 26
Plan of experiment opp. 4
Precautions in study 3, 5
Ratio in control cross 3, 4
Crossing over of B_r with certain characters 33
Culture of 2 dominant mutations 28
Curves for selection of "high lines" 12-16, 19, 21-23, 25
Curves for selection of "low lines" 6, 8-11, 18, 20, 22-24
Double crossovers between B_r and star 31
Dumpty 33
Effects of poor cultural conditions 6
Effects of selection upon Mendelian ratio 1-26
Examination for mutations 28
Extra veins 29, 30
Eyeless 3
Crosses with normal 3
Lowered viability 3, 4
Range in grade 3
Selection for excess of 4, 5, 11, 16-20, 22-24, 26
Frequency curve 4
Gynandromorphs in 102
Hereditary behavior of 2 dominant mutations 27-36
Inbreeding of brother-sister matings 28, 33
Jaunty 31, 33
Lethal effects of homozygous B_r 30
Lobed 33
Methods of study 28
Multiplied lateral bristles, B_r 28, 30, 31, 33, 35
A second chromosome character 30
Crossed with normal 30
Crossed with star 30
Good fertility and viability 35
Heterozygous dominant 30, 35
Drosphila (continued)
melanogaster (continued)
Multiplied lateral bristles (continued)
Cross of heterozygous normal and eyeless (continued)
Lethal effect when homozygous 30, 35
Linkage with star 30, 31, 33
Locus 31, 33, 35
Other crosses 33
Rate of mutation 35
Notch, a sex linked dominant 28, 29
Notch$_2$ 29-32
A second chromosome character 30
A somatic and germinal mutation 29, 30, 32, 35
Affected by cultural conditions 29
Bilateral notches 29, 30
Crossed with normal 29, 31
Dominant character 29, 35
Occurrence in heterozygous form 29, 35
Recognizable only in 1st 2 days of hatching 35
Tested with star-dichaete 30, 31
Unilateral notches 29, 30
Offsetting selective mortality 5
Precocity of female 542
Selective mortality 1, 5
Sex-linked factors 28
Sex ratio 34
Used as control 34
Variation in flies hatched per bottle 4, 5
Wild type (Plus) 33
Miniature 355, 356, 395, 396-398, 419, 422, 447, 450
Morula 420, 447
Mutations 356
Non-disjunction in 89, 355, 356
Notation 143
Partial sterility induced by X-ray treatment 363
Peach 283, 291
Percent of crossing over in X-rayed flies 361, 362
Plexus 284, 286, 288, 289, 294
Purple 284, 286, 288, 289, 293, 294, 296, 297, 397, 420, 422, 447, 450
Recording X-ray dose 356
Rough 420, 447, 449
Roughoid 283, 291
Rudimentary 395, 396, 398, 422, 447, 450
Sable 395, 396, 398, 399, 419, 422, 450
Safranin 297
Scarlet 283, 291
Scute 283, 290
Second chromosome 397, 419, 420
Semi-lethals 281
Sepia 420, 447, 449
Sex chromosomes 255
Sex linkage 356
Sooty 283, 291, 420, 447
Speck 284, 286, 288, 289, 294, 397, 419, 420, 422, 447, 450
Spineless 283, 291, 420

Drosophila (continued)
Star 281, 289, 294-297, 397, 419-422, 447, 449, 450
Sterility of vestigial flies 277, 282
Streak 397, 422, 450
Suggestion of a sterile vestigial allelomorph 277, 282
Susceptibility to X-rays 365
Technique in use of X-rays 357
Third chromosome 420
Time of X-ray treatment 359
Truncate 278, 299
Vermilion 283, 290, 395-399, 419, 422, 447, 449, 450
Vestigial 295-297, 397, 420, 447
Vestigial allelomorph linked to a lethal 282, 284, 285, 295, 296
virilis 420, 449
White 355, 395-399, 419, 421, 422, 447, 450
X chromosome 395, 399
Yellow 395-399, 419, 421, 447, 449, 450
Dual nature of grafted trees 458
Duplicate factors
In soybeans 107-109
Where there is linkage 106-115
DURRELL, L. W. 315, *320*
"Dwarf Boston" fern 78, 77, 85, 88, 89
DYAR, 541
DYER, C. L. *105*, 195, 196, 206, *211*

EAST, E. M. 104, *105*, 117, 125, 132, 145, *152*, 189, 205, *210*, 251, 315, *320*, 552, 556, *560*
EDWARDS, W. H. 529, 530, *550*
Effect of environment on polarity and symmetry 341
Effect of environmental factors in development in Planaria 351
Effect of genetically impure seedling stocks in fruit propagation 459
Egg nucleus, importance of 334
EIMER 90
ELDERTON, W. P. 65, *68*
EMERSON, R. A. 89, 93, *95*, 102, *105*, 106, 107, 110, *115*, 322, *334*, 466, 471, 474, *475*, 552, 553, 562, 563, 576, 578, *585*
ENGELMANN, T. W. 342, *354*
Environment 250
Environmental conditions, effect on graft combinations 458
Epigenesis 336
ERIKSSON 314
Erysiphe graminis on wheat 314
Eureka lemon (See lemons)
Euripus 541
European silver-spot butterfly 537
Extinction of double animal organisms 491

Factor for bitterness in sweet almond 390, 391
Factor for dwarf plants in maize 568
Factor for liguleless leaf in maize 568
Factor for purple aleurone in maize 568
FARRAR, W. 312, *320*
FEDERLEY, H. *334*

Ferns (See Nephrolepis)
Bases for classification 92, 93
Fine-striped leaf in maize 471, 475
FISCHER, E. 498, 537, 538, 547, *550*
FISH, A. 251, 260
Flatworms 339
Fluctuations 90
FOGG, L. C. 498
FOLSOM, D. 189, *211*
FREEMAN, G. F. 310, *320*
French Crab seedling stocks for apple propagation 459, 460
FROST, H. B. 102, *105*, 116, 117, 121, *152*, 284, 285, *300*
Fruit trees, variation in yield of 179
FRYER, J. C. F. 532, 536, 537, 547, *550*
FUKUYAMA, J. 175, *177*

GAINES, E. 317, 318, *320*
Gametic ratios
Calculation from zygotic ratios 106
Corresponding zygotic series 109
GARBER, R. J. 312, 316, *320*
GARNER, W. W. 121, *152*
GATES, R. R. 154, 155, 156, *167*, 234, 235, 552, *560*
Gene changes causing mutations 89, 90
Generic cross in doves 546
Genetics of curly wing in Drosophila 276-300
Geometrid moths 542
Germ plasm 338
GERNERT, W. B. 562, *585*
GEROULD, J. H. 495, 496, 499, 503, 532, *550*
Gladiolus
Bud sporting in 104
cardinalis 104
Sterile hybrids of 104
The Bride 104
tristis 104
Golden leaf in maize 475
Golden Spangled Hamburg fowl 367, 389
GOLDSCHMIDT, R. 394, 451, *457*, 496, 532, 536-539, 547, *550*
GOODALE, H. E. 38, *68*
GOODSPEED, T. H. 97, *104*, *334*
GOWEN, J. W. 179, 186, *210*, 420, 421, 448, 452, *457*, 458, 461, *465*
GOWEN, M. S. *210*
Grades of nursery stock 459
Grafting 458
Apple on pear 458
Mahaleb stocks for cherries 458
Mazzard stocks for cherries 458
Pear on apple 458
Pear on quince 458
Plum on peach 458
Prune on almond 458
Prune on apricot 458
Prune on peach 458
Roots from the scion 459, 460
GRABAU, A. W. 90, *95*
GRAVATT, F. 131, *152*
GREEN, W. J. 189, *210*

Gruber, K. 491, *493*
Guinea-pig 250
  Birth-weight 252
Guthrie, C. G. 598
Guyer, M. F. 90, *95*

Haase-Bessel, G. 226, *232*
Hagedoorn, A. L. 27, 28, *35*
Hagedoorn vorstheuvel La-Brand, C. A. *35*
Haldane, J. B. S. 106, *115*, 145, *152*, 394, *457*
Halsted, B. D. 562, *585*
Harenactis 350
Harris, J. A. 37-40, *68*, 114, *115*, 186, 191, 192, 194, 196, *210*, 462, *465*
Harrison, J. W. H. 542, *550*
Hart's-tongue fern 87
Hastina 541
Hawkins, L. A. 189, *211*
Hayes, H. K. 310, 312, 316, *320*, 552
Hedrick, U. P. 182, 183, 187, 196, 201, *210*
Hegner, R. W. 488, 489, 490, 491, 492, *493*
Hemoglobins, crystallography of 340
Hemolymph 503, 505
Henderson, L. J. 90, 91, *95*
Hereditary potentialities 338, 339
Hertwig, O. 336, *354*
Heterosis
  Due to dominant genes 151, 152
  Due to stimulating effect of dissimilar genes in hybrid condition 117
  In crosses of *Raphanus Raphanistrum*×*R. sativus* 132
  In crosses of *Raphanus Raphanistrum*, wild × cultivated 132
  In Raphanus 116-153
  In wheat 317
  In wide F_1 crosses 138
  Jones' hypothesis 138
Heterosis hypothesis 559
High Protein strain of corn 583
Hildebrandt, F. M. 189, *211*
Hill, 186
Holmes, S. J. 28
Homing pigeons 545, 546
Honey-bee 542, 547
Hopkins, F. G. 535, *550*
Hops, plot tests 194
Horse, coefficient of variation for fecundity 181
Huck, J. G. 594, *598*
Hutchison, C. B. 562, 563, *585*
Hybrid vigor (See Heterosis)
  Due to dominant genes 151, 152
  Due to heterozygosis 151
  In radish crosses 135, 151, 152
  Transmission of 152
Hybridization, increasing the difficulties of classification 93
Hybrids, chromosome behavior in 223
Hydroid 338, 339, 344, 351 (See Corymorph)
Hypothesis of qualitative nuclear division 337

Ibsen, H. L. 445, *457*
Inbreeding
  In Drosophila 117
Inbreeding (continued)
  In maize 117, 125
  In Raphanus 116
Incubating temperature for silk worm eggs 333
Indian maize 467
Inheritance of doubleness in Arcella 478, 492
Interaction of factors for pericarp color in maize 468
"Interference" 399, 422, 423
  Complete 425, 426, 455
  Curves for different amounts of 443-455
  General relations 439-451
  In chromosome I of Drosophila 432, 450
  In chromosome II of Drosophila 432, 450
  Partial 426–429, 455
Interspecific hybrids
  In crepis 212–232
Ishikawa, C. 323

Jacobson, E. 532, 536, 537, 547, *551*
Japanese turtle-dove 544
Jennings, H. S. 251, 260, 393, 394, 451, *457*, 477, 490, 491, 493, *551*
Jennings' "basic propositions" 397, 398, 454, 456
Johannsen, W. Frontispiece
Jones, D. F. 117, 119, 125, 132, 138, 143, *152*, 251, 559, *560*, 582
Jones, E. E. 1
Jones' hypothesis of heterosis 138
Junco hiemalis 534

Kains, M. G. 458, *465*
Kajanus, B. 131, *152*
Kakizaki, Yôichi 168
Kellogg, V. L. 90, *95*
Kelsey, James, A. 562, *585*
Kempton, J. H. 471, *476*, 576, *585*
Kihara, H. 315, *321*
King, H. D. 1, 2, *26*
King, W. O. R. *334*
Kirkpatrick, W. F. *550*
Klebs, G. 122, *153*
Knuth, Paul 118, *153*
Kooiman, H. N. 174, *177*
Kraus, E. J. 122, *153*
Kurtzweil, C. 310, 316, *320*

Lady fern 87
Lagging chromosomes in wheat 319
Larval blood color in Colias 503–505, 516
Lattimore, R. A. 520
Leclerc, J. A. 315, *321*
Lefevre, G. 367, *389*
Leidy, J. 488, *493*
Leighty, C. E. 262, *275*
Lemon
  Bud variation studies 188, 206
  Correlations in yield 188
  Effect of soil on yield 193, 195
  Eureka 181, 188, 195, 196, 206
  Lisbon 188, 195, 196, 206, 209
  Permanence of performance 188

Lemon (continued)
Variation in yields of clones 182
Length of day, effect upon radish 121
Lepidoptera 496, 541
Lethal factors
Balanced lethals 159, 160, 284, 285, 299
In colias (See Colias)
In Drosophila (See Drosophila)
In Oenothera
Egg lethal 156, 162, 163, 165, 166
Gametic 156, 162
Sperm lethal 156, 165
Zygotic 156, 159, 160, 165, 166
Lettuce, ruffling in "curly" forms 93
LEVINE, M. N. 305, 314, *321*
LEWIS, H. R. **37**, 38, 39, 40, *68*
LILLIE, F. R. 339, *354*
LINDSTROM, E. W. 107, *115*, 562, 563, *585*
"Linear Theory" **393**-457
Numerical discrepancies 422, 423, 446–450, 454–556
Numerical relations implied 394, 451
Relations required 403, 454
Linkage
Advantage of the backcross in analysis 106
Calculation of intensities in case of duplicate factors **106**–115
In Adzuki bean **168**–177
In Oenothera **154**–167
In *Raphanus Raphanistrum* 116, 145, 146
In soybeans 107–115
In wheat 310, 316
Independent of somatic characters involved 145
Of one member of a set of duplicate factors with a third factor **106**–115
Linkage relations of Mendelian factors in maize 468
Linkages of P_1 factor in maize 475
LIPMAN, C. B. 90, *95*
LITTLE, C. C. 1, *334*
Liverworts 339
Localization and differentiation of organs 343
Localization in cytoplasm 339, 352
LOEB, J. 333, *334*
LOTSY, J. P. 27, 28, *35*
LOVE, H. H. 262, 311, 312, *321*
LUTZ, F. E. 29, *35*
LUTZ, MISS 234
Lycaenidae 496
Lycopersicum—Solanum chimeras 103
LYNCH, C. J. 332, *334*

MACOUN, W. T. 203, 209, *210*
MCCRACKEN, I. 322, *334*
MCPHEE, H. C. 553
Mahaleb stocks for cherries 458
Maize
Aleurone 568
Brachytic 470, 475
Crinkly 93
Dilute sun-red 467, 469, 473
Dwarf 568
Effects of inbreeding 117, 125
Endosperm anomalies 102
Fine stripe 471, 475
Golden 475
Green plant 467, 469
Liguleless 568, 569
Luteus 475
Pericarp series 466–475
Plant colors 467–475
Purple plant 467
Salmon silks 475
Shrunken 568, 569
White seedlings 562–598
MAILINOWSKI, E. 131, *153*
Malva crispa
Ruffling in 93
Man
Coefficient of variation in number of children per family 181
Sickle-cell anaemia in 594-598
MANN, MARGARET C. 27, **212**
"Map distances" 421–423, 450, 451, 454
MARCHAL, E. 223, *232*
MARRYAT, D. C. E. 316, *321*
MAST, S. O. *35*, 477, 490, *493*
Maternal inheritance **322**–335 (See *Bombyx mori*)
"Deferred nuclear influence" 332
Definitions 323
Imago stage 332
Importance of nucleus 333, 334
Inheritance of color in silkworm eggs 323
Material for study 324
Methods of study 324
"Monolepsis" 323
Plastid inheritance 322
"Time of action" 323, 332–334
Voltinism 333
Matthiola 287, 299
Bud variation in 102
Delay of flowering by super-optimal temperatures 121
Maturity in insects influenced by gametogenesis 542
MAVOR, JAMES W. **355**, *366*
MAXON, W. R. 83
MAYOR, A. G. 498
Mazzard stocks for cherries 458
MEIJERE, J. C. H. DE 532, 533, 536, 537, 547, *551*
MELCHERS, L. E. 314, 317, *321*
MELHUS, I. E. 189, *211*
Mendelian heredity 146
Mendelian inheritance 251
Mendelian method of analysis, in Oenothera 156, 157
Mendelian ratio, effects of selection upon 1–26
Mendelian size factors 552
Mendelian theory 251
MEREDITH, E. T. 205, *211*

Mice, coefficient of variability for size of litter 181
Micellar structure of protoplasm 341, 342, 347, 348, 350
MILES, F. C. 562, *585*
Mildew, on wheat 314
MILL, J. S. 249
Millet 195, 208
  Plot tests in India 194
MINER, J. R. *211*
MINOT, C. S. 252, *255*
MINOT's guinea pig hypothesis 252
Modifiability of characters 116, 121, 122
Modified Mendelian ratios in Nicotiana 97–99
MOENKHAUS, W. J. *35*
Molar predeterministic theories of polarity symmetry 343
Monolepsis 323
MOORE, A. R. *334*
MORGAN, T. H. 29, *35*, 102, *105*, 233, 236, 291, *300*, 323, 332, *334*, 337, 339, 351, *353*, 355, *366*, 393, 394, 395, 397, 419, 451, 453, 454, *456*, *457*, 498, *551*
Mosaic disease in potatoes 189
MULLER, H. J. 102, *105*, 119, *153*, 277, 284, 286, *300*, 337, *354*, 399, 420, 444, 448, 453, *457*, 557, *560*
Multiple factor hypothesis for size inheritance 552, 557
MUMFORD, F. B. 367
MUNSON, J. V. 541, *551*
Mutations 89, 94
  By chromosome elimination 100, 102
  In almond 391
  In Oenothera 27
  In *Raphanus Raphanistrum* 150
  In wheat 319
  Occurrence in asexually reproducing organisms 27
  Occurrence in pure lines 27
  Point mutation in Nicotiana 100
  Resulting from new combinations of unchanged genes 27
  Two new dominant mutations in *Drosophila melanogaster* 27–36

NAKAI, T. 168
"Natural" seedlings in apple propagation 459
Nectarines, bud variation to the peach 104
Nephrolepis
  Alternation of generations 84
  Baeri 78, 79, 87, 88, 94
  Bud sports 75–95
  Cresting 75–84, 87–89, 93, 94
  Difficulties attending taxonomic work 92
  Dwarfing 78–80, 85–91, 94
  elegantissima compacta 75, 78–80, 84–89, 94
  elegantissima cristata 76–79, 81, 87, 88
  exaltata bostoniensis 75, 81, 85–88, 94
  Fertile strain 91
  Gretna 78, 79, 87, 88
  Leaf dichotomy 80, 83, 84
  Morphological studies 84
Nephrolepis (continued)
  Origin of new species 92
  Parallel variations 75, 78, 79, 84–87, 90, 94
  Piersoni 78–80, 84–88, 94
  Progressive sporting 75, 81, 87, 88, 91, 94
  Propagation 83
  Regressive varieties 84, 85, 86, 88, 94
  Reversion in 75
  Reverting leaves 75–80, 84
  Ruffling 80, 85–87, 94
  Spore sports 93, 94
  Sporelings 91–93
  Sterility in 86
  Superbissima 86
  Teratological phenomena 84
  Unnamed sports 78, 79, 86, 88
  viridissima 86
  Vivipary 75–83, 92, 94
  Wanamakeri 78, 79, 85, 88
Nicotiana 145
  macrophylla 97
  sylvestris 98
  Tabacum
    Bud variation in 97–105
    Flower-color studies 97
    Genetically distinct red flowered types 97
    Inheritance in 97–105
    Periclinal chimeras 97–105
    Propagation by cuttings 99, 100
    Ratio 9:3:4 in flower colors 97, 98
  Tabacum var. "*Cuba*" 97, 98, 100
  Tabacum var. *purpurea* 98, 100
NILES, H. E. 239, 240, *255*, 256, *260*
NILSSON-EHLE, H. 562, *585*
Nitrogenous fertilizers and rust resistance 316
Non-disjunction in Drosophila 89, 355
NORTON, J. B. 553, *560*
Notolophus (Orgyia) 541, 542
  antiqua 541, 542
  gulosa 541
  leucostigma 541
  Moulting 541

Oats (See Avena)
  Chromosome numbers 315
  Correlations of rachis internode factors 315
  Reduplication of factors 315
  Relation of chromosome number and economic value 315
  Relation of disease resistance and chromosome number 315
Oenothera
  Apparent mutants in "balanced lethal" 286
  biennis 156, 162, 166
  biennis sulfurea 156
  cana 234, 235
  candicans 234, 235
  Chlorotic forms 164
  Chromosome rings 165
  Crossing over in 154–167
    Between factor for *funifolia* and a zygytic lethal 160

Oenothera (continued)
Crossing over in (continued)
Between revolute leaves and red hypanthia 154, 159–162, 166
Between revolute leaves and red stems 154, 158, 159, 166
Between *rubricalyx* buds and *sulfurea* flower color 154, 162, 163, 166
Between *sulfurea* factor and an egg lethal 162, 163
Between *sulfurea* flower color and *nanella* stature 154, 163–166
Percentages 161–166
Crossover mutation 164
Deficiency of types due to physiological causes 164
Dihybrid ratio 161
Flat leaves 158, 162, 164
franciscana 156, 157, 164, 236
franciscana sulfurea 162, 163
gigas forms 223
Green bud cones 156, 158, 163, 165
Green hypanthium, *erythrina* 159–165
Green stems 158, 159, 163
Hookeri 283
Lamarckiana 155, 156, 159, 160, 164, 233–238, 283
Arrangement of chromosomes in mid-diakinesis 236
Assigning mutant groups to chromosomes 237
Brittle races 233, 235
Central group of mutants 236, 237
Chromosome numbers of certain types 234
CLELAND'S preparations 236
Derivations of certain mutants 234, 235
Differential growth of pollen tubes 233
Dimorphic mutants 234
Doubling of the central chromosome 238
Doubling of one chromosome 233, 234
Dwarfs 233
Extreme changes explained as modifications of Mendelian phenomena 27
Fifteen-chromosome mutants 235
Fourteen-chromosome mutants 235
Half-mutant *erythrina* 235
problandina 235
rubricalyx 235
rubrinervis 235
scindens 235
simplex 235
Heterogamy 234, 237
Homozygous alethal segregate 235
Intermediate half-mutants 235
Irregular reduction phenomena 236
Key for distinguishing groups of mutants 235
Lateral groups of mutants 236
Mutant, *albida* 234, 235
auricula 235
aurita 235
blandina 235
compacta 235
decipiens 235
delata 235
deserens 235
diluta 235, 236
distans 235, 236
elongata 235
favilla 235
flava 235
fragilis 235
funifolia 237
lactuca 235
laeta 236, 237, 238
lata 234, 235
latifrons 235
linearis 235
militaris 235
nanella 235
nitens 235, 236
oblonga 234–236
pervirens 237
scintillans 234–236
secunda 235
semi-lata 235
simplex 235, 237
spathulata 234, 235
sublinearis 235
subovata 235
tarda 235
velutina 236, 237
venusta 235
Partial sterility of pollen-grains and seeds 233
Preferential fertilization 233
Semi-gigas types 234, 237
Sesquiplex mutants 234, 235
Six main types of dimorphic mutants 234
Size of chromosomes 236
Twenty-one-chromosome types 237
Lamarckiana gigas 234
Latifrons 156
Linkage 154–167
Revolute leaves, with red hypanthia 154, 158–162, 166
Revolute leaves with red stems 154, 158–162, 166
Rubricalyx buds and sulfurea flower color 154, 162–163, 166
Sulfurea flower color and *nanella* stature 154, 163–166
liquida 234, 235
List of factors in one linkage group 165
Long styles 158, 162
nanella stature 154, 155, 158, 159, 163-166
Narrow petals 165
pallescens 234, 235
Pink bud cones 158, 163
pratincola umtant *formosa* 161, 165
Red bud cones 163, 165
Red hypanthium, *rubricalyx* 154–165
Red stems 154, 158, 159, 163, 165, 166

Oenothera (continued)
Revolute leaves, *funifolia* 154, 155, 158–166
rubricalyx 156, 157, 159, 165, 166
rubricalyx brevistylis 158
Seed germination 157, 158
Short styles 158
Studies
Material and methods 155, 158
Study of genes by Mendelian method of analysis 156, 157
sulfurea flower color 154, 156, 162–166
Suppressed basal branches, *columnaris* 165
Tall stems 158, 159, 163–165
Yellow flower *sulfurea* 156, 162–165
Oporabia
autumnata 542
autumnata×*O. dilutata* 542
dilutata 542
Chromosome numbers 542
Sex ratios 543
Optically anisotropic plant and animal tissues 342
Orange alfalfa butterfly 496
Oranges
Antelope Heights 196
Arlington 182, 184, 196
Effect of soil heterogeneity on yield 192, 193, 207
Gold Nugget strain 192
Permanence of performance 188
Thompson strain 192
Unproductive strain 192, 193
Valencia 182–184, 187, 188, 193, 195, 196, 200, 206, 207, 209
Variation in yields of clones 182
Washington Navel 182–184, 187, 192, 195, 196, 200, 205, 207, 209, 210
Orthogenesis 90-92, 94
In fossil species 94
In Nephrolepis 90, 94
OSBORN, H. F. 90, 91, *95*
Oxytricha 477, 489, 490

PAINTER, T. S. 597, *598*
PALLAS, P. S. 27, *35*
Papilio 496, 499, 532–537
aristolochiae 533
Comparisons with Colias 532–537, 547
coon 533
Genetic constitution for *P. memnon* and varieties 536, 537
hector 533
Inheritance of color pattern 499
Inhibitor factor 537
memnon 532–536, 547
memnon var. *achates* 533, 535, 547
memnon var. *agenor* 533, 535, 547
memnon var. *laomedon* 533, 535, 547
Polymorphic females 533
polytes 532–536, 547
polytes var. *cyrus* 533, 537, 547
polytes var. *romulus* 533, 535, 547
Possible phylogeny of certain forms 535
rutulus 541
Wing-tails 533, 535
Papilionidae 534
Paramecium 338, 477, 490
Pararge 541
PARKER, J. H. 310, 314, 315, 316, 317, *320*, *321*
Path coefficients 239–255
Application to causal relations 248, 249
Combining causation and correlation 241
Correlation coefficients 257, 259
Definitions 243
Degree of determination 245
Direction of influence 247, 248
General applications 240, 241
Method of multiple correlation 251, 260
Miscellaneous applications 252
NILES' asserted fallacies in the method 242, 256
Path coefficients and correlation 244, 245
Path regression 244
PEARSON'S formulae for multiple correlations and multiple regression 242, 253, 254
Precautions in applying formulae 246
Relation to multiple correlation 252, 253
Relative importance of heredity and environment 250, 251
Standard deviation of X 244
The theory as a mathematical proposition 243
WRIGHT'S summarized reply to NILES 254, 255
Pattern in organisms
Asymmetric modifications of pattern 340
Axiate or polar pattern 339, 340
Bilateral pattern 340
Combinations of patterns 340
Individual pattern 337, 338
Spiral modifications of pattern 340
Surface-interior pattern 339, 340
Peaches 458
Nectarine reverting to peach by bud variation 104
Pear 458
PEARL, R. 181, *211*, 251, 256
PEARSON, K. 65, *68*, 171, 181, 183, 242, 249, 307, *321*, 357, *366*, 461, *465*
Pelargonium zonale 102
PERCIVAL, J. 311, 312, 313, 314, *320*
Pericarp in maize 466–475
Allemorphic types 466, 467, 475
Backcross data for cherry pericarp 471–473
Backcross data for red 468–470
Brown pericarp 466, 469
Brownish modification of cherry 474
Categories of pericarp colors 475
Cherry, r^{ch} 467, 468, 471–475
Factor relations of cherry pericarp 471–474
Factor relations of red pericarp 468–471
Factorial relations of pericarp colors 466, 468
Independence of factors for red and cherry 468
Independent inheritance of Cherry and P_1 473

Pericarp in maize (continued)
Independendent inheritance (continued)
P and *A* 469, 475
P and P_1 470, 475
P and *R* 470, 475
R, P_1 and *A* 474
Inheritance of pericarp colors 466–475
Inheritance of red pericarp 466
Interaction of factors producing pericarp color 468, 475
Linkages of *P* 470, 471, 475
Linkages of P_1 475
Modification of cherry pericarp 467, 474
Mottled aleurone 471
Mutability of factor for variegated pericarp 467
Nomenclature 467
Orange 466, 469
Pericarp colors obscuring aleurone 471
Pigments in brown 468, 475
Pigments in cherry 468, 475
Pigments involved in red pericarp 467, 475
Red, *P* 466–470, 475
Red-cob white 466, 467
Relation of *A*, P_1, r^{ch} to plant and pericarp colors 474
Relation of r^{ch} to *A* 473, 474
Relation of r^{ch} to P_1 472, 473
Relation of r^{ch} to *R* 471
Relation of *P* to *A* 468, 469
Relation of *P* to P_1 469
Relation of *P* to *R* 470
Sun-red pericarp 467
Variegated 466, 469
White (colorless) 466, 469
White-capped red 469
Periclinal chimeras in *Nicotiana Tabacum* 97–105
Permanence in productivity of citrus trees 465
Perpetual heterozygote in Oenothera 156
Pe-tsai (*Brassica chinensis*), hybrid with turnip 150
PFEFFER, W. 342, *354*
Phaps chalchoptera 546
Phaseolus
angularis 168
chrysanthos 168 (See Adzuki bean)
Mungo var. *subtrilobata* 168
radiatus var. *aureus* 168
vulgaris 552–560 (See Beans)
Pheasants 90
Phyllitis (hart's tongue fern) 87
Physiological correlation 338, 339
Physiological explanation of sex-controlled heredity 339
Physiological polarity and symmetry 335–354
Pierid butterflies 495–550
Pieridae 534, 535
Pieris
oleracea 533
rapae 533, 534
PIERSON, F. R. 80, 85
PIESZCZEK, A. 528, 549, *551*
PINNEY, E. 332, *334*
Planaria 351
Planarian worm 338
Plant colors of maize 466, 467
"Plastid inheritance" 322
PLATE L. 322, *334*
PLOUGH, H. H. *300*, 355, *366*, 419, 420, 448, 452, *457*
Plum seedlings for stocks 458
Plums 458
Polarity and symmetry 336–354
Experimentally controlled 343
Reactions to gradations in physiological condition 343, 349, 350, 351–353
Polarity as an inherent property of living protoplasm 339, 342, 343, 352
Polarity distinguished from germ-plasm pattern 338
Polarized light, to detect micellar system in protoplasm 342
POLL, H. *551*
Pollen
Defective in hybrids of *Raphanus Raphanistrum* and *R. sativus* 145
Differential growth 233
Partial sterility 233
Polyhedral or wilt disease of caterpillars 500, 502
Polymorphic females in Colias and Papilio 533, 534
Polymorphism in butterflies 495
Polymorphism in Papilio 496
POMEROY, C. S. *105*, 182, 183, 184, 187, 192, 195, 196, 205, 206, *211*
Portulaca 86
Reverting branches on dwarf plants 103
Potatoes
Bud mutation in 184
Correlations in yield 187, 188
Curly dwarf disease 189
Degeneration 189
Diseases 189
Effect of disease on yield 205
Eliminating effects of soil differences 184, 188
Green Mountain 182, 187–189
Mosaic 189
No permanence in high and low selected lines 189, 193, 205
Plot tests 194, 195
Rural New Yorker 182, 187–189
Transmission of disease by aphids 189
Tuber lines 188, 190
Variation in yields of clonal varieties 182, 184, 187, 188, 190
Poultry (See Domestic Fowl)
Black Leghorn 332
Brown Leghorn 367–389
Brown Leghorn×Silver Spangled Hamburg 367
Golden Spangled Hamburgs 370
Silver Spangled Hamburg 367–389
Silver Spangled Hamburgs×Brown Leghorn 367
Spangling 367–389

Poultry (continued)
Spangling (continued)
Analyses of crosses 372–374, 378, 379, 382, 383, 386–388
Black tail 370, 372, 373, 375, 387
Characterization 367–369, 389
Crosses 370, 372, 374, 375, 378, 380, 383, 385, 386, 388
Expression of black 369–371, 373, 375–377, 381, 386
Expression of spangling 369–370, 389
Factor for 367, 369, 389
Golden-bay background 370, 378, 379, 382, 383, 385
Inheritance of black 383, 389
Multiple factors for black 369, 370, 383, 387, 389
Ratios 371, 373, 383
Rumpless 385
Sex linkage 367, 369, 370
White Leghorn 40, 66, 332
Powys 181
Preformation 336–338
PRELL, H. 531, *551*
Primula, *gigas* forms 223
Propagation of horticultural varieties of fruit trees 458
Protective mimicry 532–534
Prunes 458
PRZIBRAM, H. 341, *354*
Puccinia
coronata 315
graminis 305, 314
PUNNETT, R. C. 532, 534, 537, *551*
Pyrus malus 201 (See Apple)

Quince 458

R factor for aleurone color in maize 568
Rabbits 559
RAGIONIERI, A. 131, *153*
RAINES, M. A. 317, *321*
RANDOLPH, L. F. 562, *585*
Raphanus Raphanistrum
Abnormal characters 125, 126, 151
Abortion of flower buds 125
Albino forms 126
Anthocyan color 143, 144
Black root-color 143
Color studies 116, 119, 136
Complimentary factors for flower color 127
Conditions favoring root thickening 121
Correlation of thickness of root with time of flowering 141, 146
Cultivated varieties 118, 119, 123, 124, 127–135, 137–143, 147, 150, 152
Carrying genes for root thickening 130, 131
Early Long Scarlet 118
Early Scarlet Turnip 118, 140
Epicure 118
French Breakfast 118
Lady Finger 118
Long Black Spanish 118, 129, 139
Long White Vienna 118
Raphanus Raphanistrum (continued)
Cultivated varieties (continued)
Papery capsules of 150
Scarlet Globe 121
White China 118
Cumulative factors for root size 128
Cumulative genes for thickness of root 131
Difficulties in studying self sterility 118
Divided petals 126
Doubling in flowers 126
Earliness 136, 141, 145, 146, 148
Effect of growing conditions on time of flowering 121, 122
Effect of high temperature on time of flowering 121
Effect of length of day on growth 121
Flower color
Pink 143
Purple 117, 127
Red 143
White 117, 127
Yellow 117
Yellow, a plastid color 126, 129, 146
Gray root-color 143
Greater vigor of hybrids 123–125, 127, 129, 131, 134, 137, 138, 142, 147, 152
Heterosis and dominance of size factors in 116–153
Heterozygosity of varieties 152
Hybrid seedlings less susceptible to "damping off" 136
Improvement by hybridization 150
Indication of growth vigor 131
Isolation of lines by selfing 152
Lateness 146–148
Dominant gene for 147
Recessive gene for 148
Leaf length 120, 123, 124, 131, 132, 134
Length of root 131
Linkage of root color with size 144, 145, 152
Loss of vigor in selfed lines 152
Methods of growing and studying, in hybridity studies 119–121
Mode of branching 135
Modifiability of characters in 121, 122
Monohybrid factorial difference for root thickening and lateness 146
Mutation in 150
Natural crossing 116
Partial sterility 125, 133
Purple root-color 142–145
A sap color 143
Dominant gene for 142
Linkage with earliness 144, 145
Purpling gene in varieties not having red roots 143
Wild type 143
Reciprocal crosses correspond closely 135
Red root-color 142-145
A sap color 143
Linkage with lateness 144, 145
Simple recessive to purple 142, 143
Reflexed pedicels 126, 135
Relation of length of root to thickness 131

Raphanus Raphanistrum (continued)
Relative vigor of selfed lines and crosses 116
"Rogues" 150
Root colors 142–145
Associated with flower color 143
Root diameter 120–124, 127–131, 134, 137, 138, 142, 147
Branched roots in hybrids with *R. sativus* 130
Nearly complete dominance of wild type over cultivated 129
Root stem ratio 134, 138, 141, 146
Root thickening 144, 146, 147, 149, 150, 151
Cumulative non-allelomorphic genes for 136, 150
Dominant genes for 136, 151
Economic value 151
Root thickness recessive in certain cruciferous crosses 131
Self fertile lines hard to establish 119
Selfing 118, 119, 123-128, 139, 140, 145, 147, 149, 151, 152
Self sterility 116, 118, 119, 152
Species cross with *R. sativus* 117, 130, 132, 145
Stem diameter 120, 123, 124, 127, 129, 130, 134, 137
Sterile hybrid with cabbage 131
Sterility 145
Sunburning of seedlings 120
Superiority of certain types of roots in nature 150
Technic of selfing 118, 119
Tendency to root decay transmitted 136
Time of flowering 120, 121, 123, 131–134, 136, 137, 141, 147, 148
Earlier flowering in larger hybrids 132
Segregation of 138
Two partially dominant genes for long root 131
Unfavorable recessive genes 116
Variability of characters 117–119
Variability in F_2 hybrids 135
Vicinism 126, 149
White root-color 143
Wild types 116, 117, 120, 121, 123, 124, 127–137, 139–143, 147, 148, 150, 152
Woody capsules of wild type 150, 151
Woody-rooted condition 150
Yellow root-color 143
A recessive plastid color 145
Raphanus sativus 117, 130, 143, 145
Cross with *R. Raphanistrum* 117, 130, 132, 145
Selfing 118
Structure of capsule 151
Rats
Chromosome number 2
Males digametic 2
Modified sex ratio 1, 2
High female line 2
High male line 1, 2
Normal sex ratio 1, 2
RAWES, A. N. 204, 205, 209, *211*
Recessive genes, unfavorable effect of 116, 119
Reconstitution of parts in Polymorpha 344
Reduplication of factors
In oats 315
In wheat 311, 319, 320
REED, H. S. 182, 184, 196, *210*
REICHERT, E. T. 340, *354*
Relation between physiological gradients and hereditary constitution 343, 349
Relation of surface to polarity and symmetry 350
REMICK 251, 260
REYNOLDS, B. D. 477, 478, 490, *493*
Rhizopod 478, 491
Rhodocera rhamni 531
RIDDLE, O. 544, 545, *551*
RILEY 541
ROBERTS, E. 355, *366*, 452, *456*
ROOT, F. M. 479, *493*
ROSENBERG, O. 216, 223, *232*
ROUX 337, 339
RUCKER, E. H. 367
Rust on grains (See Puccinia)
Rust resistance (See Triticum)
RUTHVEN 90

Salmon silks in maize 475
Saltation in Nephrolepis 85, 86, 87, 90, 91, 94
SANDO, CHAS. E. 468, *476*
SAUNDERS, E. R. *300*
SAX, KARL 179, 216, 301, 302, 303, *321*, 458, 461, *465*, 552, 553, *560*
SCHULTZ, E. S. 189, *211*
SCOFIELD, C. S. 194, *210*
SCOTT, L. B. *105*, 182, 183, 184, 187, 192, 195, 205, 206, *211*
SCUDDER, S. H. 529, 531, *551*
Sea urchins 332, 338
Secondary sex characters 497
Seed germination
In Oenothera 157, 158
In wheat 304
SEITZ, A. 541, *551*
Selection
Effect of selection upon a Mendelian ratio 1–26
Modification of sex-ratio in rats 1, 2
Selective mortality in Drosophila 1, 5
Senecio vulgaris 562
Senegal turtle dove 546
Sex-controlled characters 496–498, 537, 539
Sex determination in rats 2
Sex limited variations in Pierid butterflies 495–552
Sex linkage
In Drosophila 28, 356
In poultry 367–370, 389
Man 597
Sex physiology in Lepidoptera 541
Sex ratios
In Colias 543, 549
In doves 545
In Oporabia 543

Sex ratios (continued)
Modified sex ratio in rats 1, 2
Sex reversal of dominance 498
Sexual maturity, in domestic fowl 68
SHAMEL, A. D. 104, *105*, 182, 183, 184, 187, 192, 193, 195, 196, 205, 206, 209, *211*, 465
SHAMEL, A. W. 94, *95*
SHAW, J. K. 459, 460, *465*
SHAW, T. K. 553, *560*
Sheep
Coefficient of variation for lambs per birth 181
Wool clip 186
Shrunken endosperm in maize 568
SHULL, A. F. 277
SHULL, G. H. 117, *153*, **154**, 155, 157, *167*, 235, 237, *238*, 286, 324, 553, 557, *560*
Sickle cell anaemia **596**–598
Arriving at a 1:1 ratio 596
Behaves as a single Mendelian dominant, not sex linked 596, 598
Charts showing inheritance 595, 597
Due to alteration of blood cells 594
Inheritance of sickle cells **596**–598
Occurrence only in negroes and mulattoes 594
Salient features of disease 594
Silk worm (See *Bombyx mori*)
Silver Spangled Hamburg fowl 367–389
Size factors
In Raphanus **116**–153
Location of in chromosome 145
Snakes 90
Soil heterogenity
Affecting size of apple trees 462
Influencing performanence of clonal varieties 190–200, 207, 208
Plot tests 194
Solanum-Lycopersicum chimeras 103
Somatic segregation, by chromosome elimination rather than by point mutation 102
Soybeans
Calculations of linkage from F_2 106
Calculation of linkage from F_2 trihybrid distributions 106
Difficulties in making backcrosses 106
Duplicate factors for yellow cotyledon 107
Green cotyledon 107, 108, 111–113
Green seed coat 107, 108, 111–113
Linkage of seed coat and cotyledon colors 107, 108
Yellow cotyledon 107, 108, 111–113
Yellow seed coat 107, 108, 111–113
"Spear" character in maize 582
SPILLMAN 553
Spilopelia suratensis 546
STAKMAN, E. C. 305, 314, *321*
STANDFUSS, M. 530, 531, 535, *551*
STECHE, O. *551*
Stentor 477
STEPHENS, D. E. 318, *321*
Sterility
In apple 200
Sterility (continued)
In Boston fern 86
In Drosophila 277, 282
In Raphanus 116, 118, 119, 145, 152
In wheat 301–303, 309, 311, 318, 319
STEWART, J. P. *211*
Stigmatopelia senegalensis 546
STOCKING, R. J. 490, *493*
STOUT, A. B. 118, *153*
Streptopelia
alba 545
alba×*Turtur orientales* 546
risoria 546
Breeding records 545
STUART, W. 189, *211*
STURTEVANT, A. H. 289, 291, *300*, 337, *354*, 452, 453, *457*, 542, *551*
Sun-red plant color in maize 471
Surate turtle dove 546
SURFACE, F. M. 180, 181, *211*, 553
SUTTON, ARTHUR W. 155
Symmetry in organisms
(See Polarity)
Syngamy, in Arcella 478
Syrphus flies 534
SYVERTSEN, R. C. 498

TÄCKHOLM, G. 223, *232*
TAKAHASHI, Y. 175, *177*
TALIAFERRO, W. **594**
TANAKA, Y. 322, 323, 325, *334*
Tassel seed in maize 471, 475
TEICH 541
TENNENT, D. H. *335*
TERAO, H. *335*
Terias lisa 496
Tertiary sex characters 498
Tetraploidy 223, 231
In *gigas* forms of plants 223
Theory of path coefficients **239**–255
Tilletia levis 314
Tilletia tritici 314
"Time of action" 323, 332–334
TJEBBES, K. 174, *177*
Tolman Sweet seedling stocks for apple propagation 460
Top-working
In apples 182, 183, 137
In citrus 205–207
TOYAMA, K. 322, 323, 324, *334*
TRACY, W. W., SR. 118, *153*
TREVILLIAN, J. T. 80, 81, 83, 85, 88
Trimorphism in Colias 547
Triplicate genes in maize 584
Triticum (See Wheat)
Accuracy of chromosome counts 305
Aceto-carmine used for chromosome counts 304
Agronomic varieties 313, 314
Bimodal frequency distribution 307
Bivalents 301, 303, 304, 319
Breeding resistant varieties 318, 320

Triticum (continued)
Brittleness of rachis 261
Cause of sterility 303, 304
Characteristics of *sativum* group 263
Characteristic of spelts 263
Chromosome counts 304, 306
Chromosome numbers 301–305, 307, 308, 315
Classification of characters 307
Code for descriptions of wheat hybrids 306
Coefficient of squareheadedness 263, 273
Compactness factor 265
compactum 312, 314, 217, 318
Comparison of lax spelts with lax *sativums* 274
Compatibility 304, 306, 311
Correlation
Between awn length and chromosome numbers 307
Between chromosome number and culm diameter 307
Between chromosome number and morphological and physiological characters 301–320
Between chromosome number and morphological characters 306, 315, 319
Between chromosome number and rust resistance 306, 307, 315
Between different morphological characters 306, 307, 309
Between rust resistance and length of awns 310, 317, 318
Between rust resistance and morphological characters 306, 310, 315
Correlation table for density, squareheadedness and spelting 272
Cross pollination 302
Degree of sterility 302–304
Density 262
Density also dependent on *S* factor 273
Density partially dominant over laxity 265, 274
dicoccum 311, 313–315, 318
dicoccum×*T. turgidum* 311
dicoccum×*T. vulgare* 311
Distinguishing characters of groups 307–310, 319
Division into groups 318
durum 301–305, 307–310, 312, 313, 318
Elimination of gametes 305, 319
Equational division of chromosomes 301, 319
Forms of *sativum* 264
Fourteen-chromosome wheats 301, 312, 313, 318, 319
Frequency distribution of sterility 303
Functional gametes 303, 304
Genotypes of F_2 plants 266–271
Germination 304
Heterosis 317
Homozygous segregates 302, 311, 312, 319
Intermediate chromosome numbers 304, 305, 319
Irregular behavior of chromosomes 304

Triticum (continued)
Lagging chromosomes 319
Linkages 310, 316
Mendelian segregation 311, 316
monococcum 313,
Morphological characters 302
Mutations 319
Non-functional gametes 303, 304
Physiological factors and rust susceptibility 316
Pollination 302
polonicum 304, 312, 313, 318
Ratios 311, 316
Recombinations 303, 311, 320
Reduction division 301, 319
Reduplication of factors 311, 319, 320
Relation between chromosome number and pollen grain size 319, 320
Relation of chromosome numbers to propagation 311, 315
Relation of rust resistance and bread-making qualities in cultivated wheats 314
Relation of spelt factor to rachis internode characters 261–275
Relation of spelting to density 271
Relation of spelting to squareheadedness 271
Resistance to bunt 317–320
Resitance to mildew 314, 319
Resistance to rust 302, 305, 306, 310, 312–317, 319, 332
Resistant varieties 317
Rust infection through stomates 316
sativum 261
Selective fertilization 304
Seven-chromosome group 318, 319
Similar correlations in oats 315
Spelt factor and rachis internode 261–275
Spelt factor interferes with expression of density and squareheadedness 273, 275
spelta 312, 314, 318
Spelting factor *S*, 265, 266
Spelting partially dominant over *sativum* form 265, 274
Squareheadedness 262, 265, 266, 274
Squareheadedness does not segregate in a definite ratio 266, 274
Sterility 301, 302, 305, 309, 311, 318, 319
Susceptibility to ergot 302
Taxonomic differences 307, 318
turgidum 311–313, 315, 318
Twenty-one-chromosome wheats 301, 314, 318, 319
Univalents 301, 303, 304, 311, 319
vulgare 301–305, 307–311, 314, 317, 318
vulgare×*T. durum* 302–305, 308–313, 316, 319
vulgare×*T. polonicum* 304, 305
vulgare×*T. turgidum* 312
TROUARD RIOLLE, MLLE. Y. 117, 119, 130, 132, 143, 145, 150, *153*
TROW, A. H. 562, *585*
TSCHERMAK, E. VON 312, 553, 556, 559, *560*
Tubularia 344, 351
Tumbler pigeons 546

Turnip, hybrid with pe-tsai 131, 150
Turtur
alba 545
orientalis 544, 545
orientalis×*T. alba* 545
TUTT, J. W. 541, *551*
Twin hybrids
In Drosophila 282, 299
In Oenothera 283
Types of Colias 496

UDA, HAJIME **322**, 324, *334*
Use of seedling stocks in fruit propagation 458

VALENTIN, G. 342, *354*
Variable stocks, effect on tree growth, 459, 464, 465
Variables affecting size of apple trees 460, 461, 464
Variations (See Bud sports)
Among sporelings of Boston fern 93
Categories 90, 94
Changes in chromosome number 90, 94
Fluctuations 90
Parallel variation in Nephrolepis 75, 78, 79, 84, 87, 90, 94
Progressive sporting 87, 88, 91
Recurrent variations in Nephrolepis 78, 79, 91, 94
Regressive varieties in Nephrolepis 84–86, 88, 94
Reversion in Nephrolepis 75, 83, 85, 86, 88
VAVILOV, N. I. 314–316, *321*
Vicinism, in Raphanus 126
VILMORIN 312
Vivipary, leaves of Nephrolepis 75–83, 92, 94
Voltinism in *Bombyx mori* 333
VRIES, HUGO DE 89, 155, 157, *167*, **233**, 236, *238*, 283, *300*

WAID, C. 189, *210*
WALDRON, L. R. 310, 317, *321*
WALLACE 533, 534
Walnuts 182, 200
Variation due to heterozygosity 196, 197
Variation in yield of clones of seedlings 182, 196
WARD, H. M. 316, *321*
WARD, LEONORE **276**
WARING, J. H. 184, *211*
Warning colors 534
WARREN, D. C. *35*
WATANABE, K. 322, 324, *334*
WEBBER, H. J. 202, 209, *211*, *465*
WEINSTEIN, A. 420, 448, *457*
WEISMANN, K. 336, 337
WELDON 181
WENTWORTH, E. N. 251, 260, 498, *551*
WESSLING, H. L. 315, *321*
Wheat (See Triticum)
Amby 303, 305–307, 311
Baking tests 315
Black-bearded Spelt 273
Black Persian 314
Wheat (continued)
Bread wheats 313–315
Club 264
Common squarehead 264
Common wheat 264
Crimean group 317
Dale Gloria 265
Einkorn 306, 313, 316, 318
Emmer wheats 302, 303, 311–317
Fern 317
Florence 318
Intermediate types 311
Kanred 310, 316, 317
Kota 310, 317
Kubanka 303, 305–307, 311
Little Club 306
Macaroni flour 315
Marquis 306, 317
Polish 305
Protein content 314
Quality of gluten 314, 319
Red Fife 305
Spelt 263
Turkey 267, 317, 318
Vulgare wheats 302, 303, 311–313, 316, 317
White Spelt 265
Yield of flour 314
WHIPPLE, O. B. 182, 187, 188, 189, 193, 205, *211*
White endosperm in maize 576
White Leghorn fowl 40, 66, 332
White ring-dove 544
White seedlings in barley 562
White seedlings in higher plants 562
White seedlings in maize 562–598
Albinism due to Mendelian recessive 562
Characteristics 562
Chloroplast condition 562
Comparison of germination of S_S and s_h seeds 568, 569
Correlation between white seedling and white endosperm 576, 593
Crossover percent for white seedling and yellow endosperm 576, 580, 585
Crossover percent for white seedling and yellow endosperm 580, 585
Cytological studies on albinos 562
Factor w_a 571
Factor w_b 567
Factor w_c 567
Frequent occurrence of white seedlings in corn 562
Genotype w_3w_3 565
Genotype w_4w_4 570
Genotype w_5w_5 575
Genotype w_8w_8 758
Genotype w_7w_7 582
Genotype w_6w_6 583
Genotype w_9w_9 583, 584
Lethal nature of white seedlings 563
Linkage between w_3 and y 565, 576
Low germination of white endosperm classes 579

White seedlings in maize (continued)„
Materials used 563
Methods outlined 563
Order of genes W_3, W_8 and *Y* 578–580, 582, 585
Presence in commercial varieties 562
Relation between white seedlings and other chlorophyll types 562
Stocks used for intercrosses 564
Summary of linkage tests 585
Symbols used for white seedlings 565, 567
Tests
w_3–*d* 570
w_3–l_g 569
w_3–p_r 570
w_3–*r* 569, 570
w_3–s_h 568, 569
w_8–w_a–*su* 572, 573
w_8–w_a–*y* 573
w_8–w_a–y_2 574
w_7–*y* 577
Use of heterozygous green plants 563
Variations affecting chlorophyll development 563
White seedling determined by duplicate genes 564, 565
White seedling determined by linked duplicate genes 577, 582, 583
White seedlings determined by many factors 564
White seedlings determined by simple Mendelian recessive 564, 565
White seedlings determined by single factor 563
White seedlings determined by three homozygous recessive genes 575, 584
White seedlings in maize (continued)
White seedlings determined by triplicate genes 584
White seedlings determined by two factors 565
Xenia 563
White seedlings in Senecio due to duplicate genes 562
WHITING, P. W. 498, 503
WHITMAN, C. O. 336, *354*, 544, 545, 546, *551*
WHITTEN, J. C. 203, 209, *211*
WICHERS, B. M. 87
WILDERMUTH, V. L. 498
WILSON, E. B. 339
WILSON, R. N. 498
WINKLER, H. 103, *105*
WOOD, T. B. *551*
WOODWORTH, C. M. **106**, 107, *115*
WOOLMAN, H. M. 318, *321*
WRIGHT, S. **239**, 240, 249, 250, 251, *255*, 256, *260*

Xenia in maize 563
X-ray experiment on Drosophila 355
X-ray technic, for Drosophila 356

Yellow clover butterfly 496
Yellow endosperm in maize 475
YOUNG, J. W. 514, 521, 522, 525, 547

ZWEIGELT 528
Zygotic lethals
In Oenothera 156, 159, 160, 165, 166
Zygotic ratios
Calculations of gametic ratios from 106
Derivations of formula 108, 111, 112

INFORMATION FOR CONTRIBUTORS

The length of contributions to GENETICS will not be arbitrarily limited, but articles of less than fifty pages may be expected to appear more promptly than those of greater length. The limitations as to subject-matter will be construed broadly, so that any paper of sufficient importance, whether in the field of genetics proper, of cytology, embryology, physiology, biometry, or mathematics, if of such character as to be of primary interest to the geneticist, will find here an appropriate place of publication.

Contributors are requested to observe the usual care in the preparation of manuscripts. All references to literature should cite the name of the author, followed by the year of publication, the papers so referred to being collected into a list of "Literature cited" at the end of the article. In this list great care should be taken to give titles *in full*, and to indicate accurately in Arabic numerals, the volume number, and first and last pages, and the date of publication of each paper, if published in a periodical, and the number of pages, place and date of publication and name of publisher, of each independent publication. The arrangement of this list should be alphabetical by authors, and chronological under each author.

Foot-notes, legends for figures, tabular matter, and quotations involving more than one sentence should be typewritten on separate sheets. All foot-notes should be numbered consecutively in a single series and designated by Arabic superscript numerals.

No limitation will be placed on the kind of illustration to be used, but as funds for illustration are still very limited, authors are requested to practice restraint, and to limit themselves to such amount and grade of illustration as seem positively essential to an adequate understanding of their work. The size of the type-forms of GENETICS, exclusive of the heading, is $4\frac{1}{8} \times 7$ inches and all illustrations intended for use as single plates should not exceed these dimensions or should allow of reduction to them. Folded plates may be of any desired length, horizontally, but are limited to 7 inches, vertically.

Authors will receive galley-proofs, and, if specially requested, page-proofs will be sent also, it being understood that the latter must be returned very promptly, and that no extensive change may be made in the page-proofs, which is not compensated for within the same paragraph, or in an adjacent paragraph on the same page. Changes from copy will be charged against the author.

Contributors will receive 50 reprints of their papers, with covers, free of charge, provided not fewer than 100 are ordered. If a less number is desired, one-half the total cost of their manufacture will be charged to the author. Additional copies may be secured at actual cost of manufacture, provided these are ordered when the corrected galley-proofs are returned.

Manuscripts and all editorial correspondence should be addressed to the Managing Editor, DR. GEORGE H. SHULL, 60 Jefferson Road, Princeton, New Jersey, U. S. A.

GENETICS, NOVEMBER, 1923

TABLE OF CONTENTS

PAGE

GEROULD, JOHN H., Inheritance of white wing color, a sex-limited (sex-controlled) variation in yellow Pierid butterflies 495

SAX, KARL, The association of size differences with seed-coat pattern and pigmentation in *Phaseolus vulgaris* 552

DEMEREC, M., Inheritance of white seedlings in maize 561

TALIAFERRO, W. H., and HUCK, J. G., The inheritance of sickle-cell anaemia in man 594

C30